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THE LIFE-HISTORY OF THE EMPEROR DRAGONFLY *ANAX IMPERATOR* LEACH (ODONATA: AESHNIDAE)

By PHILIP S. CORBET

*Department of Zoology, University of Cambridge**

(With Plates 1-3 and 22 Figures in the Text)

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INTRODUCTION

Although nearly three centuries have passed since Swammerdam (1669) remarked upon our ignorance of the subject, very little succinct information exists today upon the duration of the larval stages of dragonflies under natural conditions. Apart from the contribution of Münchberg (1931) to the ecology of certain East German Aeshnidae, it seems that there have been no productive attempts to use quantitative methods to determine rates of growth. Wesenberg-Lund (1913)

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gives values for the larval duration of several species in Denmark, and Portmann (1921) made a larval study of *Anax imperator* Leach in Switzerland, but in both cases the absence of quantitative data prevents verification or precise criticism of the results. Buchholtz (1951) made a length-frequency analysis of a larval sample of *Agrion splendens* (Harris) in Germany, but her data are not sufficiently extensive to permit more than a tentative conclusion to be drawn as to larval duration.

During the period 1950-53 the writer studied the life-histories of several British Odonata with the view of determining the principal ecological factors controlling the time of appearance of the adult stage. In the process of this work, particular attention was paid to the emperor dragonfly, *Anax imperator* Leach, because for several reasons it is singularly well suited as a subject for field study. Although the principal aim of its study was to determine rates of growth and emergence times, opportunity was afforded to obtain information upon other aspects of its natural history, and it has been thought desirable to include these in a single communication. It is hoped that such a procedure will make available a framework of a dragonfly life-history which may be of comparative assistance in interpreting the ecology of other spring species (see Corbet 1954) more difficult to deal with in the field.

A. imperator is the largest species of the British Aeshnidae. It is widely distributed throughout Europe, and a subspecies assigned to it occurs in the Ethiopian Region. In England it is locally common south of Yorkshire. The flying season extends from early June until August.

From 1950 to 1953 observations were made on a population existing at high density in a small Berkshire pond, the site of two previous studies (Corbet 1951, 1952). Although results obtained from this habitat have been allowed to contribute to more general conclusions, it is of course possible that the pond may have been atypical in some important respects. Until many habitats can be studied in comparable detail, this possibility must remain. Such an objection, however, is better regarded as a limitation of the ecological method, since the nature of a habitat determines the type and extent of the information which can be ascertained from it. It would be impossible, for example, to attempt exhaustive, daily collections of exuviae at Wicken Fen, Cambridgeshire; yet, at present, such collections are the only means of obtaining an accurate measure of daily emergence potential.

In the following account only passing mention is made of larval food: analyses of faecal pellets indicate that the prey varies widely in constitution and that there is a seasonal variation in the species taken as food. In the habitats selected for study it seems likely that the food-supply was super-abundant and was not therefore a limiting ecological factor. At present, however, little is known about food preferences of dragonflies, and it may be that the non-random movements of larvae observed at certain times of year are related to the distribution of prey organisms.

The physical features of the habitat have been described in order to provide points of reference to specify larval movement and distribution. In addition, the main plant zones have been dealt with since these play a prominent part as larval

micro-habitats; this has necessarily involved a brief mention of substrata. Reference has also been made to the characteristics of the heath land, immediately surrounding the pond, which has been the site of adult studies involving this and other species.

Owing to the wide variability encountered in some of the material, it has often been necessary to collect extensive quantitative data before reaching a conclusion. For the most part, the raw data have been analysed and expressed in the form of tables or figures. But in a few cases tables of results have been deposited in the library of the Freshwater Biological Association, The Ferry House, Ambleside, Westmorland, where they may be consulted on request; such results are indicated in the text by the abbreviation 'MS, F.B.A.'.

All times have been expressed as British Summer Time; this is one hour in advance of Greenwich Mean Time.

The post-embryonic stages of Odonata in this and subsequent papers will be referred to as 'larvae', in contradistinction to the traditional terminology of 'nymphs'. This has been done to conform with current views on the evolution of the pupal stage (Hinton 1948).

THE HABITAT

The population which was the main subject of this study existed in the 'Fish Pond', Wokefield Common, some six miles south-west of Reading, Berkshire (Normal National Grid Reference: 46/531662).

Wokefield Common is a plateau of Tertiary sands and clays covered by a thin veneer of gravel. The Fish Pond was made more than 150 years ago by the damming of a small, internal drainage stream arising from the top of the plateau. The dam was placed immediately below the first exposure of clay, so that the shallow end of the pond rests on gravel and the deeper end on clay. The depth of water varies seasonally, but is prevented from exceeding about 2 m at its deepest point by an outlet pipe put in when the dam was reinforced in 1930. In summer the water level seldom falls more than 1 m below the maximum, but in exceptionally dry years the area of the pond may be almost halved. From November until April the water is usually at its maximum height. In winter the pond frequently supports a firm cover of ice. About 50 years ago, soon after its last use as a sheep-dip, the pond was drained and cleaned. As far as can be ascertained, it has since remained undisturbed save for the strengthening of the dam in 1930.

The aquatic plants form distinct regions in which larvae of different ages segregate. Fig. 1 shows the distribution of the typical plant zones, and the depth, in May 1951, when the water level lay some 5 cm below the winter maximum. In this instance, the level was unusually high for the time of year.

The shallow northern region (Fig. 1, A) has a gravel floor with little silt; this supports a thick sward of *Littorella uniflora* (L.). Fall of water level in this region results in progressive exposure of the gravel beach visible in the foreground of Plate 1 *A*. Immediately to the south of A are two floating tongues of *Hypericum*

elodes L. which project inwards from western and eastern shores. These bog mats, composing region B, serve to separate A from the deeper, southern part of the pond, C, in which clay and coarse organic silt predominate as bottom deposits. Here, *Potamogeton natans* L. occupies the middle part of the pond (Plate 1 *B*); around its margins are small patches of *Eleogiton fluitans* (L.) and *Myriophyllum alterniflorum* DC. Along the margin of the dam, which forms the southern shore, grow patches of *Glyceria fluitans* (L.) and *Hypericum*. Much of the *Hypericum* at the southern end has been blown there in small, floating clumps and derives from the exposed margins of the bog mats in region B.

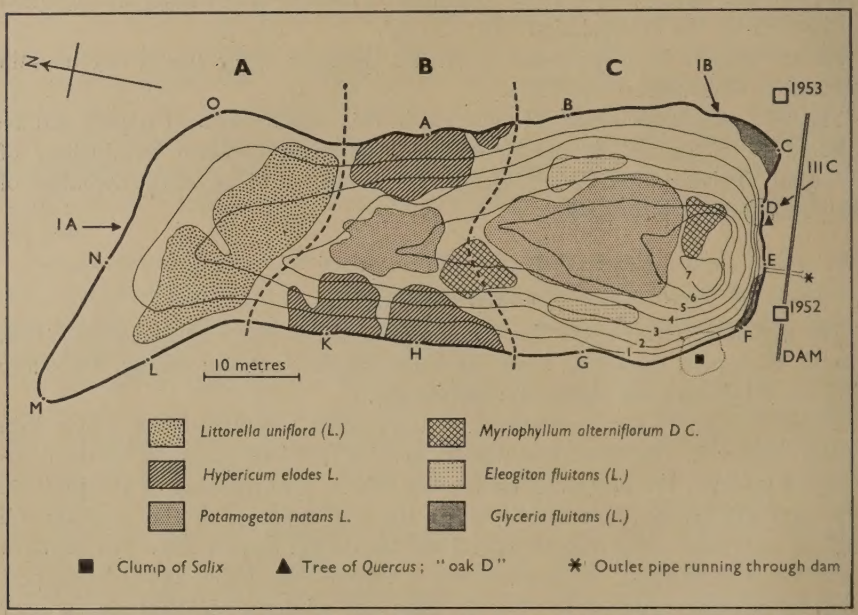

Fig. 1. Scale plan of the Fish Pond, showing the depth and the principal plant zones in May 1951. Contours are labelled in feet, and the water level was then about 6 inches higher than is usual for that time of year. The letters A to O, around the perimeter, are inserted to facilitate later reference to regions of the pond. The arrows and Roman numerals indicate the positions from which three of the Plates were taken. Two squares at the southern end of the pond represent the positions of the nests of predatory blackbirds in 1952 and 1953, respectively; both nests were in bushes of *Rubus*.

The marginal plants are worthy of mention since they influence the distribution of emergence sites. *Eleocharis palustris* (L.), *Trichophorum caespitosum* (L.) and *Juncus articulatus* L. are the principal plants in regions A and B. They occur also in region C, in company with small patches of *Carex nigra* (L.) and *Juncus effusus* L.; it is in this region that the outcrop of clay is found. In the south-western corner grow thick clumps of *Salix*, *Sambucus* and *Rubus*, and two large trees of *Quercus* stand at the eastern end of the dam.

Surrounding the pond is a gravel heath. The ground vegetation consists chiefly of *Calluna*, *Erica* and *Pteridium*, with *Ulex* and *Cytisus* in more exposed situations. At one time this land was thickly wooded with naturally sown *Pinus* but, after

A. The Fish Pond, Wokefield Common, Berkshire, 26 May 1953, viewed from the northern end. The expanse of water in the foreground covers the *Littorella* zone. In the middle distance are the two *Hypericum* mats, and behind them the main patch of *Potamogeton*. Two large oak trees growing on the dam form the background to the left, and on the right is a prominent clump of sallows.

Photos: S. Beaufoy

B. The Fish Pond 26 May 1953, viewed from between B and C, looking south-west. The path running along the dam is visible in this picture. From left to right are: *Glyceria* south-east, oak D, the dam, and the main clump of sallows. Immediately to the right of oak D stands a tall bramble bush which harboured the nest of a pair of predatory blackbirds in 1952. Behind and to the left of oak D was the thermograph used to obtain the data in Fig. 19. In the right foreground is the southern tongue of the central *Potamogeton*.

(*Facing p.* 4)

being clear-felled during the 1914-18 period, it has been colonized by a secondary growth of scattered *Betula* and *Pinus*.

Plates 1 and 3*C* show the Fish Pond from different aspects. The positions from which these photographs were taken are made clear in Fig. 1. The expanse of water in the foreground of Plate 1 *A* is about 0·5 m deep in May and covers the *Littorella* zone. In the middle distance can be seen the two *Hypericum* bog mats and behind them, in water about 1·2 m deep, lies the main patch of *Potamogeton*. Two large trees of *Quercus* growing on the dam form the background to the left, and on the right is a prominent clump of *Salix*. The trees of *Pinus*, *Betula* and *Quercus* forming the horizon in the centre are situated along the margins of the stream valley which continues southwards behind the dam.

THE EGG STAGE

The female dragonfly inserts the eggs into floating debris or the tissues of water plants. At the Fish Pond most oviposition takes place in the *Potamogeton* zone, perhaps in part due to its immunity from human disturbance, although the *Hypericum* mats are also used. Newly emerged females have been found by dissection to be reproductively immature; they return to the water to oviposit about 2 weeks after emergence (see Table 1). The latest date for oviposition in any year

Table 1. *Dates of emergence, oviposition and hatching at the Fish Pond*

		1950	1951	1952	1953	Average
I.	First date of emergence	28 May	5 June	17 May	25 May	
II.	Last date of emergence	–	12 July	5 July	7 July	
III.	Duration of emergence (days)	–	38	50	44	44·0
IV.	First date of oviposition	10 June	18 June	2 June	10 June	
V.	Maturation period in days (interval between lines I and IV)	13	13	16	16	14·5
VI.	First date instar 2 larvae observed	-	13 July	25 June	2 July	
VII.	Duration of egg development in days (interval between lines IV and VI)	–	26	23	22	23·7

is difficult to identify on account of low adult density and possible migration; furthermore, activity and dispersal of this species prohibit the estimation of longevity by capture-recapture methods. Observations suggest, however, that individual females continue to oviposit for about 2 weeks; emergence lasts about 6 weeks every year (Table 1) and oviposition usually extends over a period of about 8 weeks, from early June until early August.

The eggs are situated favourably for rapid development, being in the region of highest temperature and light intensity. Portmann (1921) demonstrated that these two environmental factors influence the rate of egg development, although the design of his experiments did not allow their effects to be assessed independ-

ently. Table 1 shows that, at the Fish Pond, eggs hatch in slightly over 3 weeks. The absence of newly hatched (instar 2) larvae from samples from September onwards makes it unlikely that eggs laid late in the season are capable of overwintering and then hatching in the following spring. The temperature of the surface water during June and July, when most of a year-group of eggs is laid, has a range of about 16 to 30° C. This contrasts markedly with the bottom water since thermal stratification develops rapidly in warm weather. It appears that stratification at the Fish Pond is more pronounced in regions sheltered by plants; in open water an unbroken thermal gradient is found (Fig. 2). Thermal gradients of this order

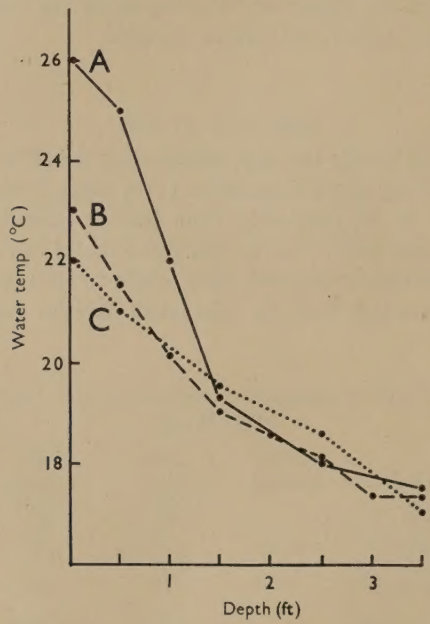

Fig. 2. Thermal stratification at the Fish Pond.
A. *Potamogeton* zone, 17 July 1951, 1800 B.S.T. A still, warm day with no wind; stratification well developed.
B. *Potamogeton* zone, 10 July 1951, 1600 B.S.T. A warm day with a strong wind; incipient stratification.
C. Open water, 10 July 1951, 1700 B.S.T. Weather as B; unbroken thermal gradient.

have been encountered in several lentic habitats studied and, in this connection, it may be remarked that the demersal eggs of exophytic Anisoptera probably take considerably longer to hatch than those developing at the surface. Another factor which may influence rate of hatching is the lower concentration of dissolved oxygen in the bottom water. In *Anax imperator* the extended period of oviposition, followed by direct development of the egg, must contribute significantly to the wide variation in size encountered in the larval population.

The egg of *A. imperator* is equipped with a blade-like extension of tissue projecting beyond the anterior pole (Robert 1939). This structure is double-layered

and takes the form of a truncated cone through which the larva passes when hatching (Corbet 1955*b*). It has been suggested that this cone may serve to prevent the egg from being enclosed by overgrowth of the surrounding plant tissue (Robert 1939). It may have another function in providing a means of anchorage for eggs laid in thin, floating leaves.

LARVAL DEVELOPMENT

(*a*) *Methods*

The growth and distribution of larvae were studied by making length-frequency analyses of samples taken from the population at regular intervals. A stout hand-net was used for collecting larvae. This had a triangular rim supporting coarse netting of 1 mm mesh. The straight leading edge, provided by the triangular frame, proved superior to a curved one when working close to the bottom, especially when this was colonized by a small plant like *Littorella*, whereas the leading corners facilitated penetration of dense accumulations of weed, such as *Hypericum* or *Potamogeton*. The mesh of the netting, while fine enough to retain newly hatched larvae, was nevertheless sufficiently coarse to allow a strong current of water to pass through the net, thereby preventing the escape of active, full-grown individuals.

In summer it was usually possible to reach all regions of the pond by wading waist-deep, but this could not be done in winter with the pond severely swollen and often covered by a thick layer of ice. Under these conditions, after the ice had been removed from the sampling area, a waterproof 'frog-man' suit was worn as a protection against the cold. Samples were then obtained in the usual way. It is difficult to overrate the importance of such equipment for this type of work. Before it became available attempts were made to collect from a rubber dinghy, to use a drag-net on wheels, and finally to wade without waterproof clothing, but all these methods proved unsatisfactory.

The dredged material was washed in a white enamel tray and the larvae removed for classification and measurement. They were then placed in a shallow dish of water and their lengths determined with callipers and a millimetre scale. The length recorded was the distance, to the nearest whole millimetre, between the anterior extremity of the head (excluding the antennae) and the distal tips of the paraprocts. This method of ascertaining size is probably the most practicable for field purposes, especially when studying the Aeshnidae in which the body-length increases greatly at each moult. Measurement of head-width provides a more accurate index of size, since this dimension undergoes negligible variation within an instar, but as a field method it becomes impracticable for use with large samples owing to the need for several micrometer scales to accommodate larvae of different sizes, and to the difficulty of keeping small, living larvae within a restricted optical plane for measurement. In addition to length, the number of larvae in the final instar was recorded. The parameters calculated from these samples appear in Table 2. The statistical methods used are those described by Simpson & Roe (1939).

Table 2. *Population parameters calculated from larval samples from the Fish Pond*

Each one of the five groups of samples is concerned with a single generation. Each sample includes one age-group only. Plant zones have been abbreviated as follows: *G, Glyceria* (south-east corner, between B and D); *H, Hypericum*; *L, Littorella*; *P, Potamogeton*.

x = larval length in millimetres

						Values of x:		Plant zones sampled			
		N	$\bar{x}$	σ	σM	Least	Greatest	*P*	*H*	*L*	*G*
1949	10 Aug.	103	11·68	4·12	0·20	3	23	+	+		
	10 Sept.	113	17·48	6·20	0·58	6	34	+	+		
	9 Oct.	95	19·47	6·69	0·69	4	43	+	+		
	10 Nov.	32	20·16	4·52	0·80	12	33	+			
1950	20 May	13	23·85	10·73	2·98	10	44		+		
	10 June	25	31·84	6·19	1·24	19	43		+		
	25 June	33	36·21	7·38	1·28	22	45		+		
1950	10 Aug.	193	12·30	3·43	0·25	2	24	+	+		
	10 Sept.	104	15·46	3·82	0·37	7	23	+	+		
	10 Oct.	87	18·56	6·69	0·72	6	37	+	+		
	17 Nov.	96	23·78	6·42	0·66	8	41			+	
	29 Dec.	61	24·18	6·01	0·77	12	44			+	
1951	17 Jan.	71	22·25	5·92	0·70	7	37			+	
	17 Feb.	97	25·93	6·54	0·66	13	43			+	
	17 Mar.	101	24·59	6·35	0·63	10	39			+	
	15 Apr.	78	24·62	6·46	0·73	12	40		+	+	
	6 May	238	23·48	6·18	0·40	10	44	+	+	+	
	17 May	79	23·42	6·91	0·78	11	45		+		
	19 June	219	27·32	5·22	0·35	14	44		+	+	
	16 July	300	36·08	5·71	0·33	20	51	+	+	+	
1952	3 Apr.	26	20·69	7·25	1·42	11	41			+	
	26 May	19	24·95	4·34	1·00	18	32				+
	6 June	115	26·94	5·86	0·55	16	41		+	+	
1952	25 Aug.	40	11·70	3·88	0·62	2	19	+			
	27 Oct.	221	19·44	7·21	0·48	6	41	+	+	+	
1953	30 Mar.	67	19·13	8·15	1·00	6	41	+	+	+	
	17 June	146	29·47	5·58	0·46	14	41	+	+	+	
	29 Aug.	52	49·50	6·16	0·85	34	55	+	+	+	
1953	29 Aug.	133	13·09	4·06	0·35	6	26	+	+	+	

After a complete sample had been collected and measured, larvae were returned to the plant-zones from which they had been obtained. Except for the samples taken in December 1950 and January 1951, larvae were returned within 24 hours of collection. On these two occasions they were returned 10 and 3 days, respectively, after sampling. In this respect, the procedure differed from that of Münchberg (1931) who distributed the measured larvae amongst habitats in which he had not previously taken samples.

It should be noted that, after the main programme of monthly sampling had been completed, three large samples of larvae were removed for experimental

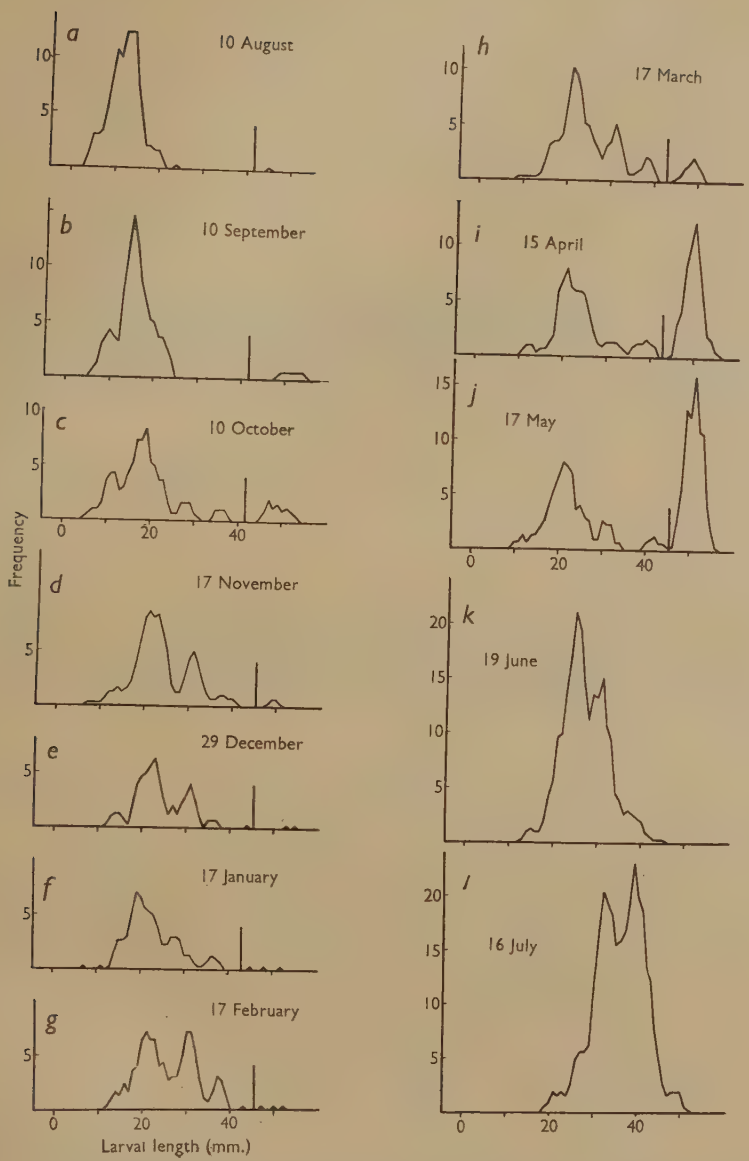

Fig. 3. Length-frequency distributions of larval samples from Fish Pond, smoothed by a moving average of three. A vertical line separates the two age-groups. *a-e*, 1950; *f-l*, 1951.

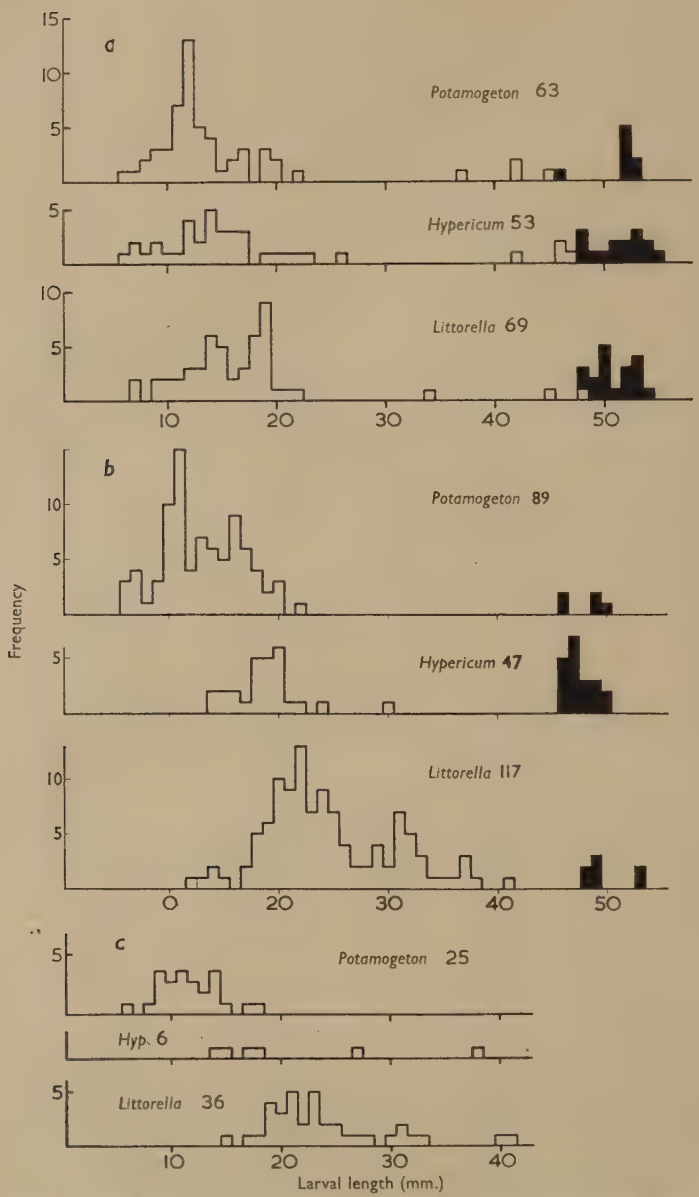

Fig. 4. Samples of larvae from the Fish Pond. *a*, 185 larvae on 29 August 1953; *b*, 253 larvae on 27 October 1952; *c*, 67 larvae on 30 March 1953 (junior age-group only).

Larvae of the senior age-group, in the final instar, have been recorded in black. *b* shows the size gradient set up amongst larvae of the junior age-group as a result of dispersal away from the oviposition sites in the *Potamogeton*; this can still be recognized in the following spring (*c*).

purposes. The material removed comprised 250-300 larvae (instars 2-4) on 21 July 1951, about 100 (instars 2-4) on 1 August 1951, and 121 (112 penultimate and 9 final instar) on 16 July 1952. Larvae of the sizes collected in July and August 1951 were extremely abundant, the earlier quantity being secured with ease in 30 minutes. Removal of the sample taken in July 1952 might be expected to have had a greater quantitative effect upon subsequent observations. Yet, information on mortality during metamorphosis obtained in 1953 (p. 37) indicates that the removal of such an amount could not have affected the numbers emerging by more than 2%.

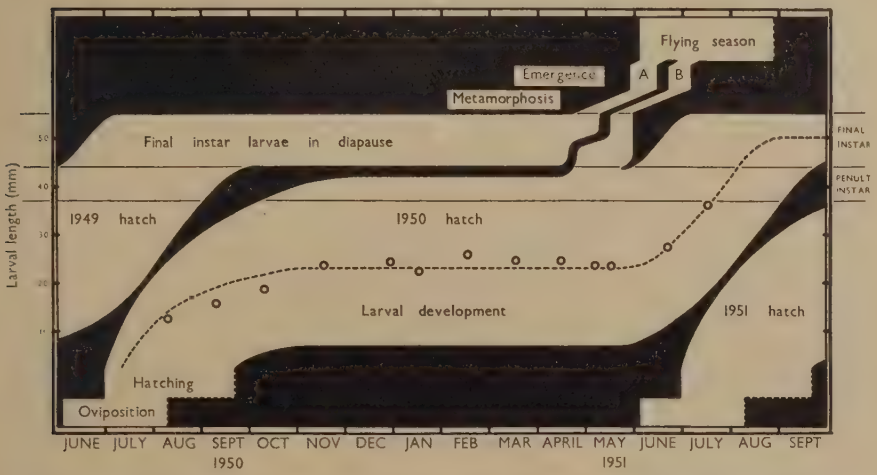

Fig. 5. Diagram to illustrate seasonal growth at the Fish Pond. The arithmetic means of samples of the 1950 hatch (Fig. 3) are indicated by circles. The associated dotted line is an approximation to the average growth-rate of the larval population. The black areas separate populations hatching in different years. The extent of the white areas indicates the extremes of size encountered within an age-group. For example precocious members of the 1950 hatch reach the penultimate instar in early October 1950, but the most backward ones not until September 1951. Most of an age-group enter the final instar in August and September one year after hatching from the egg; these spend the winter in diapause and emerge early the following year (emergence-group A). The few that enter the final instar before 1 June forgo diapause and emerge later the same year (emergence-group B). Thus adults flying in 1951 derive partly from the 1949 hatch (A) and partly from the 1950 hatch (B). This figure is semi-diagrammatic, but is based on the sample data in Table 2. The validity of the calculated growth-rate is discussed in the text.

(*b*) *Duration of larval stage*

It has already been shown that: (*a*) emergence of the adult stage is restricted in time and occurs in late May, June and early July (Table 1); (*b*) oviposition occurs from early June to early August; (*c*) the eggs develop without delay. If these facts are taken into consideration, the size distribution of larvae in the sample taken on 17 May 1951 (Fig. 3*j*) makes it clear that the duration of larval life is usually about 2 years. Furthermore, if the samples taken on 29 August 1953 (Fig. 4*a*) and

27 October 1952 (Fig. 4*b*) are considered as an extrapolation of the trends shown by those of 19 June (Fig. 3*k*) and 16 July 1951 (Fig. 3*l*), it can be seen that the final larval instar is usually entered in late summer or autumn, approximately 13 months after hatching of the eggs and 9 months before emergence (Fig. 5). Although this general scheme of the life-history has been found to hold good throughout the period of study, the situation is complicated by two circumstances: non-random spatial distribution of larvae in relation to size, and errors inherent in the methods used for computing growth-rates. These features, although necessarily investigated concurrently, will be dealt with separately.

Since about two years are required for larval development, at most times the larval population is composite, consisting of two age-groups, separated temporally by one year. It is necessary to separate these age-groups before estimates of growth-rate can be made. In recent years problems of a similar type have received the attention of many authors, mainly those concerned with the study of fish populations. It is instructive, especially in the case of insects, to consider more nicely what is meant by the term 'age-group'. With equal logical foundation it can be used to denote a population component which (*a*) hatches from the egg, or (*b*) undergoes eclosion to the adult stage, in the same year. In both (*a*) and (*b*) a stage in the life-history is arbitrarily selected to be a criterion of contemporaneity. Clearly the usefulness of any stage as a time-marker will depend upon its duration relative to that of the total life-history. In *Anax imperator* (*a*) and, to a certain extent, (*b*) are useful in this respect. It is important, however, that there should be no confusion about which stage is the definitive one, in case there is a size-overlap between the temporally-separated populations. For example, if definitions (*a*) and (*b*) were both to be respected, a larva completing its development exceptionally in one year (instead of the normal two) would, at various times during its life, be assigned to two different age-groups, a situation presenting a logical paradox. Therefore, to make the position clear, members of (*a*) will be termed an 'age-group' and those of (*b*) an 'emergence-group'.

Owing to the overlap in size which occurs between precocious members of the junior, and retarded members of the senior, age-group, no dimensional criterion for separation will be completely accurate. There are, however, certain times of year when age-groups or emergence-groups can be recognized unequivocally. In June two emergence-groups are present and easily recognizable: the senior group is represented by final instar larvae undergoing metamorphosis, by adults, and by eggs; and the junior group by half-grown larvae. In August and September it is generally possible to identify larval age-groups by inspection, at any rate in samples of only 100 to 200 larvae (Fig. 3, *a* and *b*). Later, the procedure becomes less simple owing to rapid growth of the junior age-group, some members of which appear able to enter the final instar either in their first autumn or their first spring. Inspection of winter larval samples and analyses of emergence curves indicate that this precocious component is small, constituting about 5% of an emergence-group.

Harding (1949) has demonstrated the usefulness of probability paper for resolv-

ing polymodality in overlapping frequency distributions. In the present instance, however, this method is not sufficiently rewarding to merit its application. The principal reason for this appears to be that the two age-groups are differentially represented in samples, due to uneven habitat distribution, and this introduces a qualitative element into the interpretation of samples. In addition, the use of an arithmetic abscissa scale in a case where dimension increases geometrically with every ecdysis results in instar groups (within an age-group) masquerading as separate populations. In the rare instances in which these factors are not operative (Fig. 3, *a*, *b*, *j* and *k*), identification of the separate groups is patent from inspection.

Since about 9 months, or slightly less than half the larval life, is spent in the final instar, it has been found practicable to select this instar as the criterion for diagnosis from September until June, inclusive. During this period, larvae in the final instar represent the senior emergence-group and consist largely (about 95%) of the senior age-group. The remaining larvae comprise the junior emergence-group and nearly the whole of the junior age-group. In July and August the delimitation of the two age-groups is obvious. The point of separation between the two populations, according to the criteria mentioned above, has been indicated in each of the length-frequency histograms by a vertical line.

(*c*) *Habitat distribution*

Conclusions concerning larval habitat distribution have been based upon differential size and instar distribution in contemporary samples from different plant zones. The three plant zones, *Potamogeton*, *Hypericum* and *Littorella* (see Fig. 1) were chosen empirically for the expedient collection of samples in the field. The *Potamogeton* zone comprises the southern patch in the centre of region C (Plate 1 *B*); the *Hypericum*, the eastern and western bog mats in region B; and the *Littorella*, region A. In the following account the two age-groups have been considered separately.

From early July until September, eggs are hatching amongst the surface vegetation, mainly the *Potamogeton*. Hatching probably attains a peak rate soon after commencing, since the time-frequency curve for hatching may be expected to inherit the form of the corresponding curve for emergence (Fig. 12). In late July newly hatched (instar 2) larvae are abundant amongst the stems and leaves of the *Potamogeton*, usually within about 15 cm of the surface. As hatching continues, a marked size-gradient is set up. This is shown in an early stage of development by a sample taken on 29 August 1953 (Fig. 4*a*) when the mean larval length was 13·1 mm. Later, it becomes well-established, as demonstrated by a sample taken on 27 October 1952 (Fig. 4*b*) when the mean length was 19·4 mm. On this date the differences between the mean lengths for the three samples, considered *inter se*, can be regarded as highly significant (Table 3). While this size-gradient persists the largest larvae (of the junior age-group) are found in the *Littorella*, the zone furthest from the *Potamogeton*.

It seems reasonable to suppose that this gradient is the result of dispersal away from oviposition centres which have become regions of exceptionally high density.

Besides relieving overcrowding, this movement may be of adaptive significance in reducing cannibalism (see p. 16), by effecting the separation of larvae widely different in size. It is also possible that the distribution of prey organisms may be a contributing factor. From Fig. 4*b* it appears that most of the movement responsible for this uneven distribution takes place amongst larvae of between 10 and 20 mm (*ca.* instars 9 to 11). If samples representative of the junior age-group are to be taken in late summer or autumn, allowance must be made for this non-random distribution.

Table 3. *Habitat distribution of larvae in the same age-group; comparisons of samples from different plant zones*

The central cells contain values for the mean length of each sample, with the size of the sample in parentheses. Differences exceeding the conventional level of significance are shown in bold type.

	Zones compared:				
	Potamogeton	*Hypericum*	*Littorella*	$d/\sigma d$	*P*
15 Apr. 51		23·60 (25)	24·98 (40)	0·827	>0·9
6 May 51		22·97 (88)	24·06 (116)	1·250	0·40
	24·38 (13)	22·97 (88)		0·732	>0·9
	24·38 (13)		24·06 (116)	0·119	>0·9
6 June 52		25·18 (40)	28·36 (75)	**3·260**	ca. $\mathbf{10^{-3}}$
17 June 53	27·64 (39)		30·19 (102)	**2·486**	ca. $\mathbf{10^{-2}}$
19 June 53		28·05 (104)	26·84 (104)	0·728	>0·9
16 July 51	37·13 (80)		35·20 (150)	**2·406**	ca. $\mathbf{10^{-2}}$
	37·13 (80)	36·58 (57)		0·501	>0·9
		36·58 (57)	35·20 (150)	1·724	0·11
29 Aug. 53		13·53 (34)	15·27 (48)	1·847	0·10
	12·88 (51)		15·27 (48)	**3·311**	ca. $\mathbf{10^{-3}}$
	12·88 (51)	13·53 (34)		0·714	>0·9
27 Oct. 52	13·01 (84)		24·49 (110)	**15·741**	ca. $\mathbf{10^{-20}}$
	13·01 (84)	18·85 (27)		**7·385**	ca. $\mathbf{10^{-10}}$
		18·85 (27)	24·49 (110)	**4·823**	ca. $\mathbf{10^{-6}}$
30 Mar. 53	11·44 (25)		24·08 (36)	**9·469**	ca. $\mathbf{10^{-12}}$

The size-gradient established in autumn by dispersal from oviposition sites can still be recognized in the following spring. Although the numbers involved are too small to permit of rigorous comparison, this is indicated by three samples taken on 30 March 1953 (Fig. 4*c*). Samples on 15 April and 6 May 1951 (Table 3) do not show size differences of a significant level between zones, but those on 6 June 1952 and 17 June 1953 suggest that sometimes an expression of the autumn distribution may persist until mid-June. From the samples taken on 16 July 1951 it can be seen that the size-gradient has disappeared. Indeed, there are indications that it may have become reversed, since the mean length of larvae from the *Potamogeton* exceeds that of those from the *Littorella*. The level of significance is not such that this difference can be considered firmly established, but the

possibility that larvae may grow more quickly in the surface regions (*Potamogeton*) than on the bottom (*Littorella*) owing to thermal stratification in summer, is one that should be given attention, since such a situation would result in a reversal of the autumn size-gradient. Further work is needed on this aspect of larval life.

Of the three plant zones dealt with at the Fish Pond, it appears that during the first year of larval life the *Hypericum* will yield a sample most representative of the age-group. The exception to this statement is provided by the first week or two of larval life, before dispersal from the *Potamogeton* has begun. Unfortunately, thickness of the vegetation makes it difficult to collect large samples from the *Hypericum*.

Table 4. *Habitat distribution of final instar larvae; comparisons of samples from different plant zones*

Samples (1), (2) and (3) compare the proportion of final instar larvae *within* an age-group. The remaining samples were taken when the senior age-group was deemed to consist entirely of final instar larvae; these compare the proportion *between* age-groups. Sample (7) is placed after (6) because it preceded emergence by only 15 days, whereas (6) did so by 30 days.

		Plant zone	*N*	Number in final instar	% in final instar	Average % in final instar
(1)	16 July 51	*Potamogeton*	80	6	8·5	
		Hypericum	57	3	5·3	4·2
		Littorella	150	3	2·0	
(2)	29 Aug. 53	*Potamogeton*	12	8	66·7	
		Hypericum	19	15	79·4	80·7
		Littorella	21	19	90·9	
(3)	11 Sept. 51	*Potamogeton*	12	9	75·0	
		Hypericum	37	30	80·1	76·0
		Littorella	26	18	69·2	
(4)	27 Oct. 52	*Potamogeton*	89	5	5·6	
		Hypericum	47	20	42·6	12·6
		Littorella	117	7	6·0	
(5)	15 Apr. 51	*Hypericum*	85	47	55·2	42·2
		Littorella	50	10	20·0	
(6)	6 May 51	*Hypericum*	120	29	24·2	13·8
		Littorella	120	4	3·3	
(7)	2 May 52	*Glyceria*	205	200	97·6	
		Hypericum	33	32	97·0	93·2
		Littorella	12	1	8·3	
(8)	20 May 50	*Hypericum*	100	87	87·0	

Final instar larvae can be recognized unequivocally by their length (45 mm and over) and by the size of the wing-sheaths (Corbet 1955*b*). About 5% of the junior emergence-group have entered the final instar by mid-July, about 75% by the end of August, and probably 100% by the end of September (Table 4). The possibility of a size overlap between age-groups makes it impossible to discern accurately when ecdysis is completed since the final instar itself has been selected as the criterion of the senior age-group after September. Amongst the junior emergence-group (apart from a small fraction of precocious larvae which moults to the final instar in April and May and thereby effects a transition to the senior emergence-group), it appears that ecdysis to the final instar begins in July, attains a peak

rate in mid-August and is completed in September. The reason for this apparently discontinuous pattern of ecdysis is not understood.

By the end of October, when virtually the whole of an age-group has achieved the final instar, there is a well-defined aggregation of larvae in the *Hypericum* zone (Table 4). This aggregation becomes very marked towards late autumn. Final instar larvae were abundant amongst the submerged mats of *Hypericum* when collections were made on 29 November 1951 and 10 February 1952, but were sparsely represented elsewhere. They were uncommon in samples from the *Littorella* in the previous winter from November to February (Fig. 3, *d* to *g*). The aggregation of final instar larvae in the *Hypericum* persists throughout the winter and can still be discerned in spring, as evidenced by samples taken on 15 April and 6 May 1951 (Table 4). It seems certain that the autumn accumulation of larvae in the *Hypericum* must be due to active habitat selection, although the features of this zone which serve to attract or arrest moving larvae are not known. Probably further light could be thrown on this problem by conducting similar studies in habitats containing different plant zones.

(*d*) *Coloration*

Young larvae of *Anax imperator* possess a striking and characteristic colour pattern made up of black and white transverse bands. During development, the banded pattern is gradually replaced by the greenish, mottled coloration of the older larva. Loss of banding begins in larvae 5 mm in length; about 50% are banded at 12 mm, and none at 20 mm (Corbet 1955*b*). Larvae may retain the juvenile coloration for the first year of life. During this period they are known to be subject to predation by larger individuals: faecal pellets of the senior age-group collected in August 1952 contained fragments of larvae belonging to the junior age-group. Thus, it is suggested that banding may afford protection against predation by the senior age-group. This is a possibility amenable to quantitative verification in the field. Breder (1948) has shown that light passing through a wind-rippled water surface tends to throw a pattern of light and dark stripes upon a uniformly-coloured object. It is therefore not unreasonable to suppose that, for animals living near the surface of exposed aquatic habitats, a pattern of pale and dark transverse bands may have disruptive properties. Preliminary observations upon the incidence of juvenile banding in other British species of Aeshnidae lend support to this thesis, and suggest that the size at which banding is lost bears a relationship to the normal duration of larval life. Thus *Aeshna grandis* (L.), which may require 3 or more years to attain maturity (Münchberg 1931), retains a banded coloration for about 2 years, whereas a uni-voltine species, *A. mixta* Latreille (Münchberg 1931), only shows incipient banding in the second larval instar (Gardner 1950).

(*e*) *Growth-rate*

In studies of the present type, growth-rates are usually calculated by the comparison of successive sample means for some dimension affected by growth. Two

groups of aquatic insects which have been treated in this way are the Plecoptera (Hynes 1941, Brinck 1949) and the Ephemeroptera (Moon 1939, Rawlinson 1939, Harker 1952). Unless the individuals are of a known age this method is, at the best, approximate, but it is perhaps not generally realized that, especially in the case of insects, it is subject to substantial qualifying errors which are independent of individual variation. If a sampling method deals only with the larval stage of an insect (omitting the egg and adult stages), then the hatching of eggs between two successive samples will have the effect of lowering the mean length of the second sample. In such a case, a comparison of sample means will give an erroneous estimate for growth-rate and one which falls short of the true value. This type of error must always exist in any population of unmarked individuals receiving an unclassified influx of younger forms. An error similar to this in principle can affect growth-rate estimations when part of the larval population is emerging to the adult stage. Here, again, the result is to depress the estimate of growth-rate in the residual larval population, since it is the individuals growing most rapidly that have passed beyond the scope of the sampling method. In both these cases

Table 5. *Collections of newly hatched larvae from the* Potamogeton *zone in 1953*

	Instar 2	Instar 3	*N*
27, 29, 30 June, 1 July	0	0	0
2 July	6	0	6
3 July	16	0	16
4 July	15	0	15
5 July	No collection		
6 July	42	2	44
7 July	46	5	51
8 July	59	6	65

the true value for larval growth-rate is depressed: in the first instance by the addition of small individuals, and in the second by the removal of large ones. A further source of error can exist when a diapause stage is intercalated during larval development. Here, estimates for growth are reduced because the largest individuals, which have attained the diapause stage, mark time. This situation can be regarded as an extreme example of the effect produced when successive stages in a life-history have different thermal coefficients for growth.

Visible larval growth is limited to a period from May to October, and shows a well-marked summer maximum (see Fig. 5). Newly hatched larvae grow rapidly during the first summer, the maximum growth-rate being such that larvae hatching in early July may achieve the penultimate, and perhaps in rare instances the final, instar before the onset of winter prevents further growth. This fact has a bearing upon the size-overlap between the age-groups. The short series of samples recorded in Table 5 indicates that in early July 1953 about 3 days only were spent in instar 2. For the reasons given above, the true value for average larval growth in summer cannot be ascertained from the data, since the rate of hatching is un-

known. However, it must lie between the rate indicated by the successive sample means and that shown by successive length maxima. It therefore amounts to about 7 mm a month. Such a rate is equivalent to increases in body-length of 600%, 50% and 30%, respectively, in the first 3 months of larval life. The apparent increase in growth-rate between October and November (Fig. 5) is probably a reflection of the removal of the retarding influence caused by hatching of the eggs.

Sample means show considerable fluctuation during the winter. Indeed, those for January and February 1951 differ to an extent that must be regarded as significant ($d/\sigma_d = 4{\cdot}713$, for which P is about 10^{-6}). These fluctuations are probably due mainly to errors caused by unconscious selective sampling, but it is manifest that they could have an important effect upon the interpretation of samples, especially in winter when these are typically small and often drawn from a region dictated by the expediency of ice-breaking. It seems unlikely, however, that growth occurs in winter under natural conditions; in the laboratory, larvae have shown an inability to complete ecdysis at a temperature of 6° C or less. Nevertheless, feeding continues at this time, as evidenced by faecal pellets voided by larvae collected on 10 February 1952. This is perhaps to be expected, since no well-developed fat body has been recognized in the larvae of Odonata. It is possible that active habitat selection may be responsible for the fluctuations in size observed during the winter but, in the light of the available data, it is difficult to imagine the form that this might assume. At present, this question must remain open.

When growth is resumed in spring, precocious penultimate instar larvae (of the junior age-group) enter the final instar. Ecdysis can be discerned in the field by discovery of exuviae and teneral* final instar larvae; evidence for assigning a large proportion of the moulting larvae to the junior age-group is based upon a consideration of growth-rates and larval size distribution shown by samples taken the previous summer and autumn. This entry to the final instar has the immediate effect of lowering the mean length of the junior age-group since this, by definition, does not include final instar larvae (see p. 13) from September to June. Larvae which succeed in achieving the final instar before the end of May undergo metamorphosis and emerge without delay. This has been established by gaining recaptures of marked larvae as final instar exuviae, and is dealt with on p. 38. By June, therefore, the remaining larval population is homogeneous, and sample means can be used with confidence to estimate growth. Between 19 June and 17 July 1951 the average growth was about 9 mm, or 30% of body-length, and may have exceeded this rate in August. At this stage, such a rate involves an average of about two ecdyses a month. Towards the end of the summer, accumulation of larvae in the final instar prohibits the further use of sample means to determine growth-rate. By mid-July, approximately one year after hatching, the most advanced members of an age-group are adults just embarking upon their flying season, whereas the hindermost are larvae about 18 mm long. The latter now

* 'Teneral' is used to describe newly moulted larvae or adults in which dark pigment has not yet been deposited in the cuticle. In larvae of *Anax imperator* the teneral stage lasts about 6 hours at 15° C.

grow rapidly and it must be rare for any larva to fail to reach the final instar in its second autumn. As the eggs begin to hatch, the larvae which comprised the junior now become the senior age-group. The second winter is spent in the final instar in which, at this season, a diapause is developed. No visible growth is manifested in this stage until the advent of metamorphosis in the following spring. Emergence then follows directly, occurring some 23 months after hatching of the eggs.

(*f*) *Discussion*

The only other study of the duration of larval life in *A. imperator* known to the writer is that undertaken by Portmann (1921). Portmann studied a population in a brick-pond near Basel, Switzerland, for two years and concluded from his observations that *A. imperator* was uni-voltine ('einjährig'), the egg stage lasting from 2 to 4 weeks and the larval life about 10 months. He found (1921, p. 31) that the eggs were laid mainly in June and July and that in early August the larvae were mostly between 8 and 10 mm, the maximum length being 22 mm. By the end of August they were 'middle-sized' and in November were distributed evenly between 24 and 45 mm, although the 'smallest instars' were sometimes encountered in autumn after an unusually protracted oviposition season.

Up to this point, the larval growth-rate seems to correspond closely with that exhibited by the population at the Fish Pond. But Portmann then remarks that the remaining larval growth was completed rapidly in early spring, so that 'a great number of large larvae was found towards the end of March'. At this time, 'it was rare to find a larva that was not full-grown'. Emergence began in late May and early June, as at the Fish Pond. No length-frequency data are included, and it appears that the values quoted were derived from inspection. It is therefore impossible to effect a rigorous comparison between Portmann's findings and those of the present study. Nevertheless, the rapid growth proposed in early spring (despite the similar emergence period) contrasts strongly with data from the Fish Pond, and it is suggested that there are more reasonable interpretations of Portmann's observations than the ones he gives.

In August, soon after hatching, larvae of the junior age-group are abundant in the surface vegetation. At this time they outnumber those of the senior age-group to an extent such that a large sample can consist almost entirely of the junior age-group; this situation is illustrated by the sample of 10 August 1950 (Fig. 3*a*). Thus it would be easy, when sampling in early August, to gain the impression that a population consisted of one age-group only. That this is not so is demonstrated by the sample of 29 August 1953 (Fig. 4*a*).

In spring the pattern of larval distribution in the surface vegetation (especially the *Hypericum*) has changed. The junior age-group, besides having become numerically reduced, has also become dispersed, whereas the senior age-group has undergone concentration. Furthermore, final instar larvae congregate in dense masses in the surface vegetation when metamorphosis is in progress in April and May. Thus samples from this region in spring can be strongly prejudicial to the

senior age-group. Indeed a sample of 100 larvae taken from the *Hypericum* zone on 20 May 1950 (Fig. 6), before uneven larval distribution was suspected, included only about 13% of the junior age-group, and as a result it was thought that the usual larval duration was one year. Again on 2 May 1952 only 6·8% of a sample of 238 larvae from the western *Hypericum* and southern *Glyceria* consisted of the junior age-group. It is noteworthy that in most habitats the *Hypericum* and *Glyceria* zones (or ones similar to them in position) are so disposed as to receive greatest attention during marginal sampling. It is therefore suggested that, with regard to the data available, Portmann's observations are more likely to be the result of differential habitat distribution than an indication of rapid larval growth in early spring. Were uni-voltinism the rule rather than the exception in Switzerland, emergence might be expected to begin later than in England. As it is, the emergence periods in the two countries, and also in East Germany (Münchberg 1932), correspond closely. For the reasons given above it is

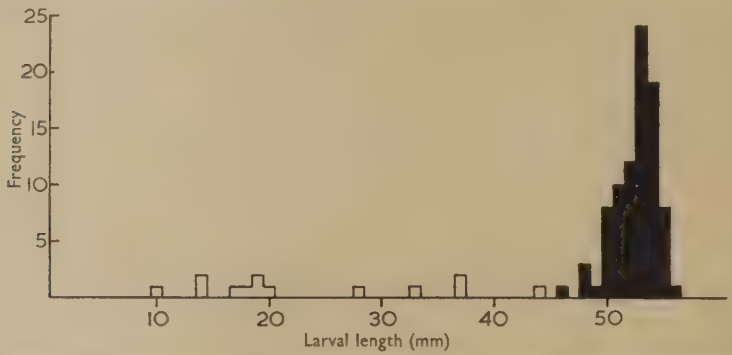

Fig. 6. Sample of 100 larvae from the Fish Pond, 20 May 1950. Larvae in the final instar have been recorded in black. This sample was taken from the *Hypericum* zone 8 days before emergence began; it is thus strongly biased in favour of the senior age-group.

considered that *Anax imperator* may well be semi-voltine (biennial) in Switzerland, and that its uni-voltinism there has yet to be established.

At this stage it is pertinent to mention the only other concise record of larval seasonal distribution available from Europe. Dr K. Lems (personal communication) obtained three larvae, each 24 mm long, from 'different places around Winterswijk', Holland, in the latter half of April 1952. At these habitats most of the adults emerged in May. That these larvae would have been unable to achieve the final instar during the emergence period is beyond reasonable doubt. They must, therefore, have belonged to a junior emergence-group at least 7 months old. The larval length corresponds closely to the mean value (24·6 mm) of this age-group observed at the Fish Pond on 15 April 1951 (Table 2).

Larval samples from other habitats in England (MS, F.B.A.) have seldom been large enough to allow firm conclusions to be drawn upon age-group distribution. In no case, however, do they contradict the interpretation of the life-history based upon observations made at the Fish Pond. Two of these samples are shown as

length-frequency histograms in Fig. 7. The population at Withermore Common, Bournemouth, Hampshire, was sampled to investigate the possibility that *A. imperator* might be uni-voltine in the south of England. If, however, allowance is made for the fact that only a small patch of littoral *Potamogeton* was accessible for sampling, it is clear that a senior age-group is represented. The size distribution of the junior age-group indicates that a mass hatch from eggs had recently taken place (21 larvae were in instar 2, and 32 were in instar 3), and it is impossible that the larvae of above 30 mm could have belonged to the hatching age-group, since the emergence period at Withermore Common is not significantly earlier than at

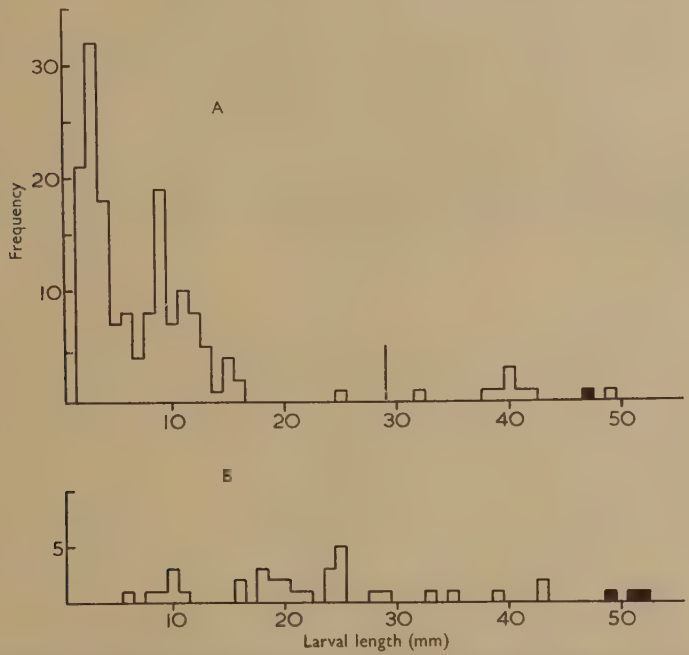

Fig. 7. Samples of larvae from other habitats. A, 165 larvae from Withermore Common Pond, Bournemouth (Nat. grid. ref. 40/610932), 23 August 1952; a vertical line separates the two age-groups. B, 37 larvae from Colmans Moor gravel pit, Woodley (Nat. grid. ref. 47/751731), 22 August 1952. Final instar larvae are shown in black.

the Fish Pond (F. C. Fraser, personal communication). The population at Colmans Moor, Woodley, Berkshire, also closely resembles that at the Fish Pond with respect to the position and duration of the emergence period; hence, although the sample is too small for the age-groups to be resolved, the size range of the larvae in August shows that more than one age-group must be present.

Although more extensive sampling is needed before a general statement can be made, there is at present no reason to suppose that the larval duration varies much in England, save perhaps to undergo extension in the north, or in small, unproductive habitats with a low annual heat budget. The size distribution of

larvae in the junior age-group may vary considerably (cf. Fig. 7). In species laying non-diapause eggs, this is clearly determined by the temporal distribution of oviposition which, in its turn, may depend upon whether a habitat receives eggs mainly from a synchronized population of residents or from temporally dispersed immigrants. It is possible that these two cases are represented by Withermore Common and Colmans Moor respectively.

It has been shown that, at the Fish Pond, *Anax imperator* is usually semi-voltine, requiring two years for larval development, but that it may occasionally be univoltine. Notwithstanding the long life-history, larval growth is rapid and limited to 6 months each year. Monthly recordings of water temperature suggest that the 'lower temperature threshold' for growth may approximate to 10° C, but it is possible that this may not be the same for all larval instars. Studies of seasonal growth in other British Odonata (Corbet 1956*b*, 1957*a*, *b*) and in East German species (Münchberg 1931) indicate that the developmental zero and the thermal growth coefficient of *A. imperator* are relatively high. The capacity for rapid growth amongst members of the genus *Anax* has been discussed by Brimley (1904) and Calvert (1929, 1934).

METAMORPHOSIS

(*a*) *Progress*

It is important to distinguish between the internal changes which directly precede the last ecdysis, and the last ecdysis itself. Here, the former are considered to constitute 'metamorphosis', whereas the mechanical processes associated with the final moult are referred to as 'emergence'.

In the field, metamorphosis can be recognized by changes in the compound eyes, wing-sheaths and labium. In order to obtain quantitative expression of its progress, the process has been divided into arbitrary stages. These have been selected principally to provide clear end-points, and it must be emphasized that the time intervals between them are not necessarily constant. The stages have been classified as follows:

Stage (1) No external sign of metamorphosis; larvae in resting state; cuticle teneral or hard.

Stage (2) Compound eyes approaching towards the mid-dorsum of the head but more than 0.25 mm apart.

Stage (3) Eyes less than 0.25 mm apart but not touching mesially.

Stage (4) Eyes touching mesially; labium larval.

Stage (5) Tissues of labium in process of retracting through sheath of larval prementum.

Stage (6) Labium of adult fully-formed and retracted, lying within sheath of larval postmentum.

These stages are illustrated in Fig. 8 and Pl. 2.

Although final instar larvae are present in all months of the year, metamorphosis is observed only from early April to early July. This temporal restriction is

effected by a diapause in the final instar, and is discussed further on p. 62.

If regular samples of final instar larvae are taken in spring and the proportions of the different stages of metamorphosis recorded, the progress of metamorphosis can be followed in the field. This method was used in May 1952 and provided the results shown in Table 6. Inspection of this table shows metamorphosis to have begun between 3 April and 2 May. On 2 May over 99% of the sample showed signs of metamorphosis and, during the next 14 days, the population advanced rapidly through the successive stages. Emergence began on 17 May. No further samples were taken after this date in order to avoid the risk of disturbing the temporal pattern of emergence. Since, however, larval mortality is continuing at an unknown rate, samples are no longer meaningful after emergence has begun because the proportion of the total emergence-group that has already emerged cannot be determined.

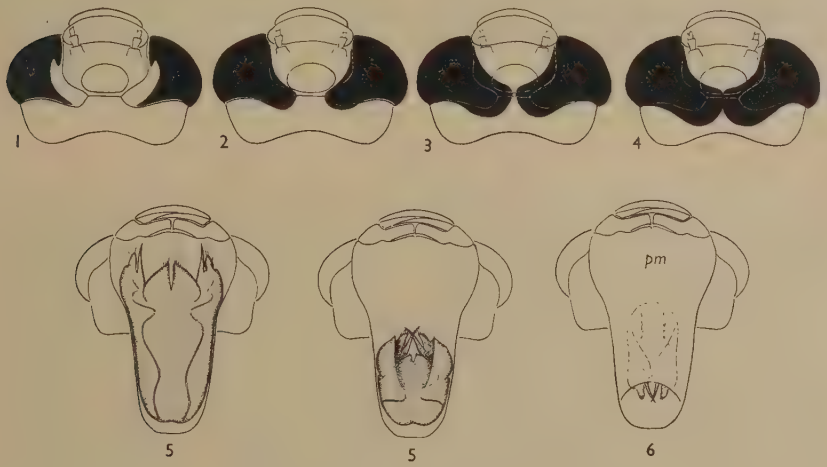

Fig. 8. Heads of final instar larvae to illustrate stages 1-6 of metamorphosis. 1-4, dorsal view; 5-6, ventral view. *pm*, larval prementum.

Although the main population advanced consistently through metamorphosis, there remained a small number of larvae in stage 1. One such larva, marked and released on 17 May 1952, emerged 40 days later. The status of these larvae is discussed on p. 38.

In 1952 little was known of the habitat distribution of final instar larvae from the time when they left their hibernating quarters, the *Hypericum* mats, until they selected emergence supports after completion of metamorphosis. It had been observed that during metamorphosis they occurred in dense aggregations amongst surface vegetation, and use was made of this knowledge to obtain samples in 1952. These were taken chiefly from the southern *Glyceria* and the eastern *Hypericum*. Since the habitat distribution of larvae was not known, however, there was no guarantee that the samples drawn were representative of the whole population.

In 1953, a procedure was adopted whereby all plant zones known to harbour larvae during metamorphosis were sampled in a standardized way. By this means it was hoped to obtain samples representative of the whole population, and also to gain an understanding of larval distribution. Larval movements were checked further by recaptures of marked specimens. An account of this part of the work appears on p. 27. These studies indicate that the results obtained by the grouping of sample data from all zones are indeed representative of the whole emergence-group.

Fig. 9 (MS, F.B.A.) shows the progress of the larval population through successive stages of metamorphosis during April and May 1953. The slightly uneven distribution of stages (1) and (2) on 26 April can be attributed to the difficulty experienced in discerning the beginning of the mesial extension of the compound eyes. Sampling was discontinued as soon as emergence began on 25 May for the same reasons as in 1952. Taking into account that successive samples were separated by intervals of about 4 days, the approximate durations of the several stages can be estimated from the intersections on the abscissa of Fig. 9. The

Table 6. *Progress of metamorphosis in a population of final instar larvae at the Fish Pond*

Percentage of the larval sample in each stage of metamorphosis.

	Number in sample	Stages of metamorphosis (1)	(2)	(3)	(4)	(5)	(6)
3 Apr.	12	100	–	–	–	–	–
2 May	233	0·4	2·6	43·8	53·2	–	–
5 May	100	1	–	28	71	–	–
9 May	94	1·1	–	8·5	90·4	–	–
13 May	100	1	–	–	99	–	–
16 May	100	3	–	–	70	16	11

thermal coefficient for metamorphosis is not known but comparison of dates for first emergence from 1950 to 1953 indicates that in 1953 pre-emergence water temperatures at the Fish Pond were of an average order. We may therefore place confidence in the following values for the approximate durations of the stages of metamorphosis in nature: stage 2, 21 days; stage 3, 4 days; stage 4, 15 days; stage 5, 1 day; stage 6, 4 days.

Thus, from the time when its external signs first become visible, metamorphosis takes about 45 days. There is negligible difference between the rates of metamorphosis for the two sexes. It is clear from Fig. 9 that the main population is responding in a very homogeneous fashion to the factors stimulating metamorphosis.

The temporal distribution of stage 1 (Fig. 9) supports the view that, while the main population is undergoing metamorphosis, a small number of larvae is entering the final instar. The synchronization shown by this second group of larvae when they metamorphose is ill-defined, as evidenced by a small sample of 4 female larvae taken from the *Potamogeton* zone on 17 June 1953 (the 24th day of emergence); these were in stages 3, 4, 5 and 6 respectively. The temporal distribution of

A

B

C

D

Photos: S. Beaufoy

A. Emergence stage 1. The larva has left the water and selected its position for emergence. It will remain motionless in this position for about three-quarters of an hour.
B. Stage 2. The resting stage. This lasts for about an hour in nature.
C. Stage 3. The adult has just withdrawn the abdomen from the exuvia, and the wings have just begun to expand; their costal margins are still corrugated. During expansion of the wings, which takes about 30 minutes, adults are very susceptible to physical damage.
D. Stage 3. The wings are fully formed, but the abdomen has not yet completely expanded.

(*Facing p. 24*)

A

B

A. Final instar larva struggling through a surface scum of sallow catkins on its way to an emergence support near oak D on 26 May 1953. The swollen wing-sheaths indicate that this larva has reached an advanced stage of metamorphosis; its left hind femur bears a mark of cellulose paint. This individual is in a position in which larvae sometimes fall a prey to blackbirds.

B. Larvae in stage 1 of emergence clustered on an emergence support, 26 May 1953. The first larva to climb the support was itself used as a support by a succeeding larva, and so on. Only the outside larva shown here will be able to complete ecdysis satisfactorily.

C *Photos: S. Beaufoy*

C. Group of sallow saplings growing in the water by oak D, 26 May 1953. These saplings comprised the sampling region used for making emergence counts (see Figs. 17 and 18). Several exuviae can be seen *in situ* on the branches of the saplings.

(*Facing p. 25*)

the emergence of this group demonstrates this point further (Fig. 14). These findings are in accord with the interpretation of the larval life-history. The first, large, homogeneous metamorphosis group may be regarded as comprising larvae nearly 2 years old that have undergone diapause the previous autumn, whereas the second, small, temporally-dispersed group represents larvae in which entry to the final instar took place in spring, and in which diapause has been averted. Such larvae are probably slightly less than 1 year old.

(*b*) *Movements and distribution during metamorphosis*

Two independent methods were used to study larval distribution during metamorphosis: (i) selective sampling in different plant zones; (ii) marking and recapturing larvae.

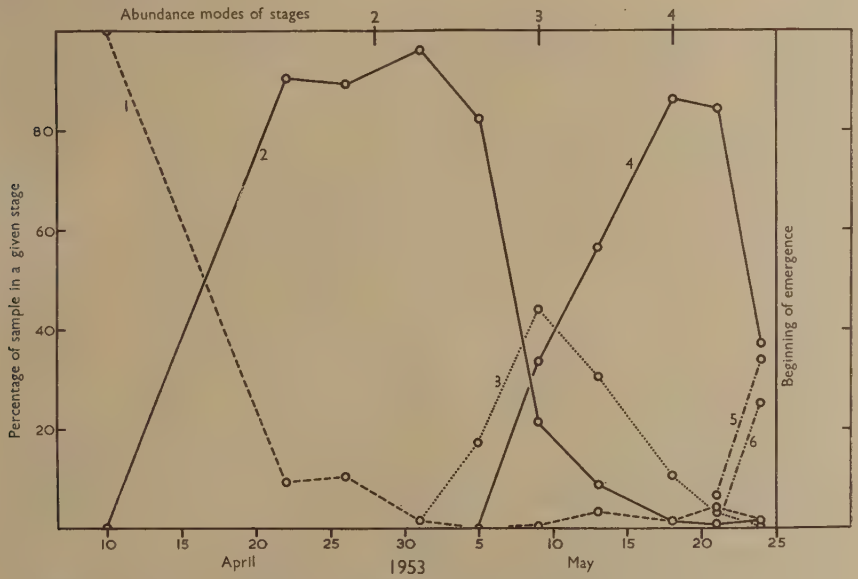

Fig. 9. The progress of a larval population through successive stages of metamorphosis.

(i) For purposes of selective sampling seven plant zones were distinguished as listed below; their disposition is made clear in Fig. 1:

Littorella (north)	*Potamogeton* (south)
Hypericum (north-west)	*Glyceria* (south-east)
Hypericum (south-west)	*Glyceria* (south)
Hypericum (east)	

Upon each occasion every plant zone was sampled using a standardized technique physically appropriate to the given zone. Thus, the numbers collected in a given zone, say the *Littorella*, on successive occasions will be comparable and can be used to determine relative densities during that period. Numbers obtained from different zones on the same occasion of sampling, however, cannot be used

to provide an index of relative abundance. This is because, owing to the structure of different plants, collecting techniques are variably efficient from one zone to another. Nevertheless, by comparing a series of collections from a single zone, it should be possible to ascertain the times of peak larval density within it. The situation is influenced by the fact that abundance of metamorphosing larvae in the surface vegetation appears to be correlated with light intensity and temperature. On dull, cold days difficulty was experienced in obtaining large samples from the *Potamogeton* zone, and it was concluded that on fine days larvae move to the surface, but that on dull ones they remain near the bottom. If this is so, samples from the *Littorella* will be unaffected by the weather since larvae are collected from the bottom in any case, but those from the *Hypericum* and, more especially, the *Potamogeton* could be expected to vary with it. It is not possible, at present,

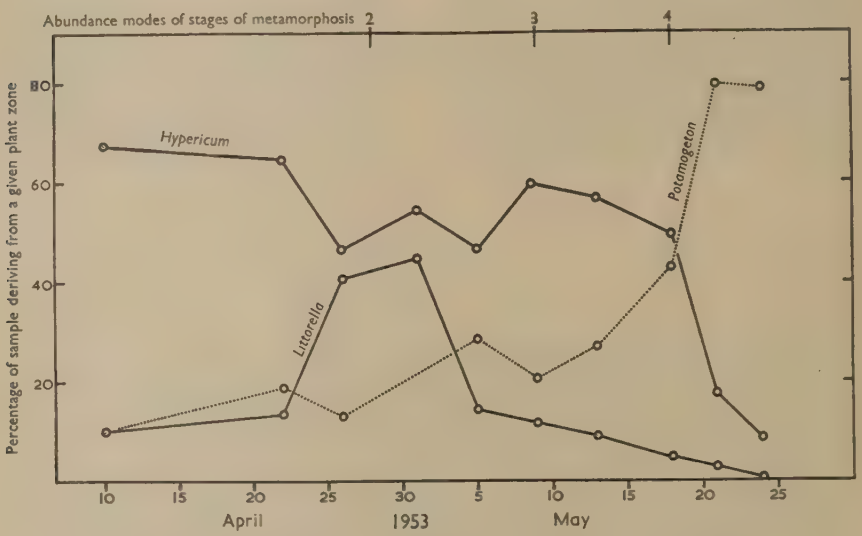

Fig. 10. Larval distribution in three plant zones during metamorphosis.

to determine the nature and extent of this vertical migration, nor the magnitude of the error caused by it but, since the results obtained by the two methods correspond closely, it appears that it cannot have been considerable. It is clear that any error arising from the 'availability' of larvae in different zones will affect comparisons of successive samples from the same zone as well as contemporary samples from different zones.

It was found that collections from the *Hypericum* mats and the *Glyceria* respectively were homogeneous *intra se*; therefore they have been grouped under these two main categories when expressing results. Samples were taken at intervals of approximately 4 days throughout the period of metamorphosis, the last one being on 24 May, one day before the first emergence. Results form the subject of Fig. 10, where they are expressed as the percentage of daily samples contributed

by each zone (raw data, MS, F.B.A.). Results from the *Glyceria* zone have been omitted; they are not instructive, save perhaps to indicate that the fall in the number of larvae in the *Potamogeton* zone after 21 May may have been due to colonization of the *Glyceria* immediately before emergence (see Table 7).

Before the onset of metamorphosis, relative density of final instar larvae is high in the *Hypericum* but low elsewhere. This is to be expected in view of the winter habitat distribution of such larvae (see p. 16). There is a distinct peak in the *Littorella* during stage 2 after which density falls at a regular rate. The *Hypericum* maintains a fairly steady density throughout the early stages of metamorphosis, although depleted in stage 2 by loss to the *Littorella*, but becomes drained of larvae towards the end of stage 4. It is clear that the migrating larvae colonize the *Potamogeton* since density in that zone rises abruptly at this time.

Table 7. *Average stage of metamorphosis reached by larvae in different plant zones at the Fish Pond, 1953*

	Total sample	*Littorella*	*Hypericum*	*Potamogeton*	*Glyceria*	Size of sample from *Glyceria*
22 Apr.	1·91	1·85	1·92	1·89	2·00	4
26 Apr.	1·89	1·88	1·89	1·94	–	–
1 May	2·00	1·96	2·04	2·00*	–	–
5 May	2·18	2·02	2·19	2·28	2·13	32
9 May	3·12	2·51	3·17	3·43	2·90	21
13 May	3·48	3·00	3·45	3·77	3·31	13
18 May	3·85	3·38	3·85	3·92	3·80	5
21 May	4·02	3·83	3·95	4·06	4·00*	1
24 May	4·83	4·00*	4·31	4·74	5·84	19

*Results from samples containing a single specimen.

(ii) Two methods have been found satisfactory for marking final instar larvae: the first makes use of cellulose paint, the second of metal strips. Of the two, cellulose paint is better for field use, on account of its quick application. For the mark to be durable the cuticle must be dry. Therefore, after collection, larvae of a zone sample were confined in dry cardboard cartons for about 10 minutes before being marked. The cuticle then possessed a waxy appearance and was ready to receive paint. Larvae were marked on the femora of the legs and also on the wing-sheaths. The latter position was less suitable due to the increase in convexity of the wing-sheaths as metamorphosis progressed. The paint was applied with a dissecting needle. After being marked, the larvae were returned to the cartons, and the paint was allowed a further 10 minutes in which to dry. The larvae were then returned to the plant zone from which they had been collected, being released from a constant, specified point within that zone. The marks given denoted date of capture, point of release and stage of metamorphosis. The brands of paint used are described elsewhere (Corbet 1952). It is unnecessary to discuss the permanence of the marks, since the proportion of marked to unmarked larvae was not of significance in this study.

Two types of metal marks were used: thin copper wire and coloured tin foil.

Thin copper wire proved suitable for re-marking recaptures to give them future distinction as individuals. A length of wire about 2 cm long was tied in a reef-knot around the femur, and the projecting ends of wire cut short with scissors. Larvae could be marked in this way at a rate of fifteen per hour. For teneral larvae, another type of mark had to be used since wire tends to sever the leg when the knot is made secure. For this purpose, tin foil was cut into strips about 1 mm wide and wound obliquely around a femur. All legs could be marked in this way. In the case of teneral larvae the best results were obtained after the femur had first been given a coat of paint. This imparted rigidity to the leg and prevented it from bending. The tin foil used was obtained from the tops of milk-bottles; these are anodized with a colour on one side. Milk-bottle tops of several colours are manufactured so that, by varying the colour, the surface coloured (outer or inner) and the position of the leg marked, it was possible to obtain an adequate number of

Table 8. *Results of marking experiment designed to study larval movements during metamorphosis. Fish Pond, April to May 1953*

Date of capture or release	Number released	Zone of recapture: Recaptured in different zone					Recaptured in same zone				
		Lit.	*Hyp.*	*Pot.*	*Glyc.*	Total	*Lit.*	*Hyp.*	*Pot.*	*Glyc.*	Total
31 Mar.	135	–	–	–	–	–	–	–	–	–	–
10 Apr.	111	–	–	–	–	–	–	–	–	–	–
22 Apr.	–	0	1	0	0	1	0	2	0	0	2
26 Apr.	118	4	2	0	0	6	0	1	0	0	1
1 May	–	6	1	0	0	7	0	4	0	0	4
5 May	140	8	2	0	0	10	1	8	0	0	9
9 May	–	5	7	0	1	13	1	10	0	0	11
13 May	148	2	3	4	0	9	1	5	1	0	7
18 May	–	0	4	5	0	9	0	20	4	1	25
21 May	179	2	2	10	1	15	0	6	9	0	15
24 May	–	1	0	15	1	17	0	3	5	0	8
Totals	968	28	22	34	3	87	3	59	19	1	82

different marks. This method has the disadvantage of being too slow for large-scale marking unless assistance is available. Working single-handed it is difficult to mark more than ten larvae in an hour.

On six occasions before emergence in 1953 larvae in routine samples were marked before being returned (Table 8). In this way 831 larvae received marks; 169, or about 20%, were recaptured before emergence. Of this number 87 were recaptured in zones other than those from which they had been released, and 82 were recaptured in the same zone. The distribution of these recaptures is itemized in Table 8. The directions taken by larvae which changed their positions after release are shown in Fig. 11. In the interpretation of this figure it must be remembered that, initially, the numbers of recaptures are very small and standard errors correspondingly high. Even if allowance is made for this, it is clear that organized movement is taking place. As before, a migration to the *Littorella* occurs during stage 1. After the onset of stage 4, recapture records show a well-

marked and abrupt migration to the *Potamogeton*. Records of visiting larvae in the *Hypericum* are variable but indicate that this zone is colonized in stage 3, during passage from the *Littorella* to the *Potamogeton*.

These results support the findings of the selective sampling method. The significant properties of the several zones which serve to attract or arrest larvae are not known. A critical study of feeding habits during metamorphosis might throw further light on this question.

It is important not to regard these findings as providing data on speed of movement. Potential speed of unidirectional larval movement is great in relation to the size of the Fish Pond. On 3 May 1953 a final instar larva was watched swimming

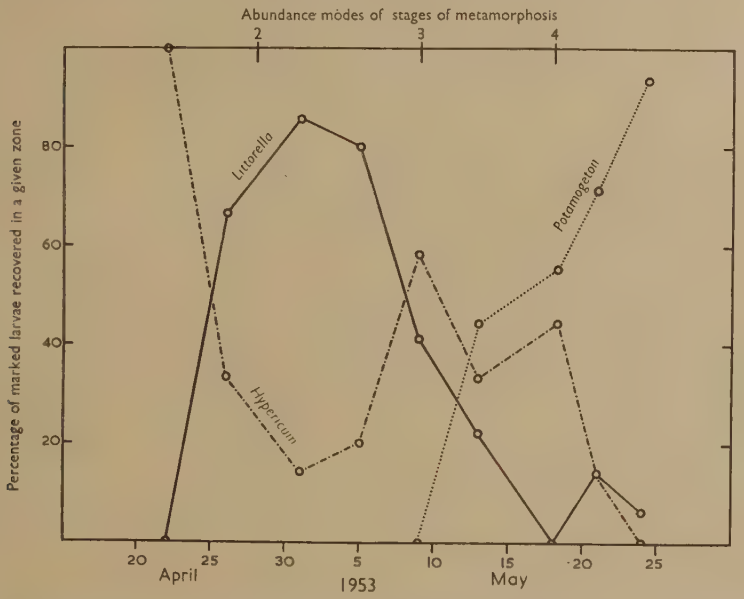

Fig. 11. Movements of marked larvae during metamorphosis. Only larvae recovered in a zone other than that of release have been recorded.

by means of jet propulsion northwards along the western shore; its rate of movement over a distance of 10 m was such as would have enabled it to cover the length of the Fish Pond in less than 1½ min.

It is clear from the results obtained at the Fish Pond that samples taken to determine the progress of metamorphosis will be influenced by the plant zones from which they are drawn. Samples from the *Littorella*, for example, will be biased in favour of stage 2, those from the *Hypericum* in favour of stage 3 and those from the *Potamogeton* in favour of stage 4. That such a bias exists is shown in Table 7 which gives the average stage of metamorphosis reached by the larvae in different zones. In the interpretation of this table it must be remembered that the mean rises irregularly on account of the uneven time intervals between the stages. The

level of metamorphosis in the *Littorella* corresponds closely to the mean until stage 2 has been passed after which it lags behind. Similarly, larvae in the *Hypericum* correspond to the mean until stage 4, when it has been shown that larvae move to the *Potamogeton*. The level of metamorphosis in the *Potamogeton*, as is to be expected, exceeds the mean during stages 2, 3 and 4. It falls short of it immediately before emergence, and this is clearly due to a movement to the *Glyceria*. Another thing that Table 7 shows is that the whole population is not involved in these movements; at the most they represent an organized, general trend.

(*c*) *Selection of emergence supports*

Most emergence is localized around the southern shore of the pond (p. 42 and Fig. 16). It is therefore desirable to know at what stage larvae move from the *Potamogeton* to the emergence sites. From the results given in Table 7 it appears that larvae begin to move to the *Glyceria* at the southern shore in stage 5. To investigate this a careful watch was maintained before emergence began at the two regions most favoured by emerging larvae: the sallow bush in the south-western corner and the sallow saplings by oak D (Plate 3*C*). Beginning on 21 May 1953, 4 days before emergence, these sites were inspected each day, from 0900 to 1800, and each night from 2200 to 0100 B.S.T. Larvae in these regions were clearly visible from the shore, and a hand-net was not needed to determine their presence. The first larvae were seen clustered around the submerged sallow stems at 2200 on 23 May, two evenings before emergence began. Most of them were clinging to submerged sticks, sub-parallel to the surface and about 7 to 15 cm below it, but some were on the vertical sides of the dam and oak D, and a few were on vertical sticks, most of these individuals being head downwards. A sample of such larvae was taken by hand, and the individuals were marked and returned. Of ten larvae, eight were in stage 6, and two in stage 5. All six of the recaptures emerged on 25 May. This information is of importance since it is known that these larvae first arrived at the emergence supports on 23 May. Of the six recoveries, five emerged from within 3 m of the position of release and one from a position about 10 m away. Another sample of larvae was marked on the night of 24 May between 2200 and 2400. In this case it was not known whether the larvae were at the emergence supports for the first or second evening.

Releases and recoveries are itemized in Table 9. From 2200 to 0100 on the last two nights before emergence, 23 and 24 May, larvae were continually arriving at the emergence supports around the southern shore. This shoreward, nocturnal movement was restricted chiefly to this region. Circuits of the pond were made frequently on both nights and other regions inspected carefully for emerging larvae. Despite this, only two larvae were seen at the shore elsewhere around the perimeter on these nights. It must be emphasized that larvae were actually arriving at the southern shore and taking up positions on the emergence supports during the period of observation. This was suggested by the sight of larvae swimming actively by jet propulsion towards the shore when the water was illuminated, and confirmed by the increasing number, new arrivals being recognized by the marks they bore.

This observation suggests that larvae are, to some extent, sensible of the position of desirable emergence sites before they reach them. It is difficult to conceive of any gradient in physical or chemical conditions which could serve as a guide to these regions at night. It is possible that larvae may respond positively to shaded regions and orientate themselves during the day-time; both the south-western sallows and oak D are probably visible to larvae around the southern edges of the *Potamogeton* (see Pl. 1 *B*). On 17 May 1952 (the day of first emergence), at about 1530, a final instar larva was seen to leave the southern *Glyceria* (Fig. 1, between E and F), swim northwards about 2 cm below the surface into open water, veer eastwards and finally take a straight course for the region shaded by oak D. On this day the trunks of the sallow saplings growing beneath the shade of oak D were clustered thickly with larvae, most of which had probably arrived there on the evening of 15 May. A rough estimate of the visual range of larvae at this time can be obtained by observing their response to sudden movements near the pond. If

Table 9. *Recaptures of larvae marked on emergence supports during the night of 24–25 May 1953*

		Males	Females	Total
LARVAE MARKED				
Stages of metamorphosis	4	0	1	1
	5	1	1	2
	6	10	13	23
	Totals	11	15	26
RECAPTURES AFTER EMERGENCE				
Dates of emergence	25 May	1	8	9
	26 May	6	1	7
	27 May	–	1	1
	30 May	1	–	1
	6 June	1	–	1
	Totals	9	10	19

a person walks quickly along the dam a few days before emergence, the surface is thrown into ripples by jets of water ejected by the larvae amongst floating vegetation swimming downwards. Such a response may occur 3 or 4 m from the stimulus, but the visual range of larvae may well exceed this distance.

The observations described above show that larvae move to emergence supports about 2 days before emergence, although a few may remain there for 3, 4 or more days before emergence (see Table 9). But this delay may be a secondary factor imposed upon the normal rhythm, perhaps when conditions become crowded, or when low air temperatures postpone emergence. Upon arrival, most larvae are in stage 6, although a few (perhaps about 12%) may be in stage 5. They move to the emergence supports by night and, having taken up their positions, usually remain there until emergence.

The remark that larvae were seen swimming towards the shore when a torch was shone has a Procrustean quality, and suggests that the light itself might have

been the source of attraction. Normally, this could not be checked, since a torch is a *sine qua non* for observation, but in this case verification was possible by recording the marked specimens which had arrived during a dark interval. This provides a fresh context in which to review a suggestion made by Klots (1943) to the effect that light could be used as a method for collecting Odonata larvae. This author remarked that many aeshnid larvae came swimming towards a strong light used for moth-collecting on the bank of a reservoir in May, to be captured with great ease. It was found that a torch produced the same effect. Now positive phototaxis is unknown amongst Odonata larvae (apart from the unconfirmed indications mentioned on p. 26), and at the Fish Pond care had to be exercised to avoid direct illumination of larvae under observation. Unless this was done, they either swam away from the light or down to the bottom of the pond. Larvae clinging to supports would promptly move to the reverse side if illuminated. Furthermore, most of the Aeshnidae appear to share with *Anax imperator* the habit of nocturnal emergence (Straub 1943), and it might be expected that they also would be similar in this respect. In the reported case there is no mention of control observations being conducted without a light. Since the time of year mentioned was appropriate it is not unreasonable to assume that the larvae observed were in the process of moving to their emergence supports. Thus, a light is still useful for collecting Odonata larvae but probably only as a means for illuminating regions in which, at restricted times of year, they have already congregated.

During many nights of nocturnal observation in 1952 and 1953, both before and during the emergence period, no larvae were seen to leave the water before emergence. This habit has been recorded frequently for captive aeshnids. A few larvae of *A. imperator* rested with head and mesothorax exposed above the water but climbed no higher. In this connection it is noteworthy that the quoted instances of this occurrence have referred to captive larvae. It is possible that in some of these cases emergence would normally have ensued but was prevented by the illumination necessary for observation. More data are needed on this question.

EMERGENCE

(*a*) *Seasonal rhythm*

Emergence, or eclosion of the imago, follows the same general pattern in all Odonata, the families differing only in detail. In its pattern of emergence, *A. imperator* is typical of the Aeshnidae. An emerging larva usually leaves the water soon after dusk and promptly climbs up a rigid, near-vertical object projecting from the water. A few minutes after a suitable position on the support has been found, the abdomen is wriggled violently from side to side. A similar behaviour pattern has been recorded for *Pyrrhosoma nymphula* (Corbet 1952); it is possible that it may test the grip of the tarsal claws and also ensure that adequate space exists for expansion of the wings. The larva then remains motionless for about three-quarters of an hour, after which the thoracic cuticle begins to split along the

ecdysial line. Straub (1943) has made a critical study of the positions adopted by different Odonata during emergence. Unlike members of the Gomphidae, Libellulidae and Coenagriidae, *Anax imperator* is specific in its requirement of an upright support of considerable rigidity. Stems of *Glyceria* and other robust monocotyledons are sometimes used as emergence supports, but in such instances several stems are drawn together and used as one. After flight of the newly emerged adult early the following morning the large exuvia* remains *in situ* on the emergence support for several days. For the first few days, rain has little effect upon its removal. In a heavy rain storm the abdomen of an exuvia becomes filled with water entering through the mid-dorsal ecdysial suture in the thorax. This exerts a downward force which serves to tighten the grip of the tarsal claws upon the support, and so resist displacement. The principal agent in the removal of exuviae is wind; a strong breeze, especially if variable in direction, can dislodge them within a few hours. Once in the water, exuviae fill with water in about 12 hours and then sink.

The diurnal rhythm of emergence, the large size and stability of exuviae, and the restricted choice of emergence supports are all factors which facilitate the quantitative study of emergence by means of daily collections of exuviae. If the emergence supports are restricted still further by artificial means, to regions accessible for collection, extensive and reliable information can be obtained concerning the absolute numbers emerging daily and annually from a given habitat. The efficiency of such a procedure depends largely upon the emergence habits of the species studied and upon the physical features of the habitat.

The technique of collecting exuviae to obtain information about emergence and relative abundance has been employed for Anisoptera by Needham & Betten (1901), Wilson (1920), Tiensuu (1935), Byers (1941) and Hornuff (1950). Of these authors only Byers, working with a population of *Pantala flavescens* (Fabricius), attempted exhaustive collections; the other studies involved collection of small, representative samples.

A preliminary study of emergence was made at the Fish Pond in 1950, when five collections of exuviae were made during the emergence period (Corbet 1951). Attempts were made to ensure that each collection was exhaustive; this permitted tentative conclusions to be reached concerning the form of the time-frequency curve for emergence and the minimum numbers emerging. From later studies, it appears almost certain that substantial emergence occurred after the last collection. In 1951 the accuracy of the method was increased. A patch of *Rubus* in the south-western corner of the pond (Fig. 1) was cut back so that the stems no longer trailed in the water and a baffle, in the form of a trellis-fence of pine-faggots, was laid along the water's edge in that region. Further trimming of marginal vegetation was done near oak D (Plate 3*C*). This effectively reduced the supports available for emerging larvae to those readily accessible for the collection of exuviae, and meant that daily collections could be made virtually exhaustive. The

* For convenience, *exuvia* is regarded as the singular form of *exuviae* (feminine plural), used here to mean cast larval skins.

baffle was liberally patronized by emerging larvae, and was renewed before emergence in 1952 and 1953.

In regions where the bank is gently sloping and few supports exist (for example, see Plate 1 *A*), larvae occasionally climbed out on to the shore and emerged on the nearest upright clump of grass, bracken or heather. The greatest distances travelled by larvae which emerged in this way in 1952 were 5 m (at K on the perimeter) and 6 m (between C and D), respectively. Such instances were rare, as shown in Fig. 16. These regions were included in the area searched daily and the exuviae could be discerned easily. It is considered very unlikely that any exuviae escaped notice in this way. As mentioned earlier (p. 31), larvae usually select their emergence supports about 2 days before emergence, and such impromptu choice of sites is rare. On tall emergence supports, such as oak D, larvae frequently climbed up to 2 m before emerging. The greatest height above the water surface at which an exuvia was found in 1952 was 5 m; to reach this position the larva must have climbed nearly 6 m over the surface of the tree.

The diurnal rhythm of emergence has two practical advantages for field study: firstly, it allows daily collections of exuviae to be made with minimum disturbance of the next emergence group and, secondly, it means that the process of emergence is split up into a discontinuous series of day-classes, a form convenient for quantitative analysis.

Collections were made daily, usually during the morning. Thus, the exuvial count for any given day has reference to the number emerging the previous evening. Occasionally, a day-group of emerging larvae becomes divided, some emerging at dusk in the usual way and the rest emerging during the morning of the following day. Such divided emergences are infrequent but, as will be made clear later (p. 45), the day-time emergence-group is composed of larvae which would normally have emerged the previous evening, and should be classified accordingly. After a divided emergence, the daily collection was made in the afternoon. It therefore comprised both sections of the day-group. Sometimes, if conditions are persistently unfavourable, it appears that some larvae are able to postpone emergence for 24 hours or longer, and in this way achieve a change of day-group. Evidence for this has been adduced from returns of marked exuviae (Table 9, p. 31). Minor fluctuations in the numbers emerging daily may be attributable to this cause.

The results of collections of exuviae made in 1951, 1952 and 1953 are given in detail in Table 10 and form the subjects of Fig. 12. In 1951, late in the emergence period, collections were not made daily. For the purpose of exhibiting the results in Fig. 12*a*, the contents of the collections made after each gap have been distributed evenly amongst the days for which records were missed. The results appear in their original form, however, in Table 10. Similar methods were employed in 1952 and 1953, save that collections were made every day during the emergence period. In 1952, emergence was considered to have finished on 5 July, and daily searches were discontinued after 15 July. When the pond was revisited on 22 August, however, a single exuvia was found, *in situ* but brittle, indicating

Table 10. *Daily collections of exuviae at the Fish Pond during the emergence period; 1951 to 1953*

Emergence began: 5 June 1951; 17 May 1952; 25 May 1953.

In 1952 and 1953 collections were made every day. In 1951, when some days were missed, (–) in a column indicates that no collection was made on the day in question; (0) indicates that a search was made but no exuviae were found. No entry is made in a year column after the end of the emergence period.

Day of emergence	1951			1952			1953		
	Males	Females	Total	Males	Females	Total	Males	Females	Total
1	19	29	48	9	9	18	141	183	324
2	130	185	315	139	177	316	585	563	1148
3	267	283	550	479	460	939	346	354	700
4	144	110	254	566	509	1075	26	36	62
5	149	156	305	59	85	144	129	102	231
6	50	47	97	294	280	574	91	102	193
7	69	70	139	220	259	479	21	32	53
8	30	21	51	93	109	202	17	15	32
9	22	17	39	35	30	65	3	2	5
10	8	6	14	20	19	39	1	1	2
11	7	6	13	6	10	16	1	4	5
12	8	6	14	9	6	15	0	2	2
13	5	4	9	4	2	6	8	0	8
14	0	1	1	1	5	6	3	3	6
15	–	–	–	3	9	12	0	3	3
16	–	–	–	4	3	7	8	11	19
17	1	5	6	1	4	5	9	17	26
18	2	3	5	3	1	4	10	13	23
19	–	–	–	3	5	8	4	0	4
20	8	5	13	11	30	41	2	0	2
21	–	–	–	25	57	82	2	2	4
22	–	–	–	4	8	12	1	2	3
23	14	10	24	6	16	22	2	4	6
24	–	–	–	8	11	19	3	3	6
25	–	–	–	6	16	22	1	2	3
26	–	–	–	18	54	72	2	3	5
27	–	–	–	20	51	71	3	0	3
28	10	15	25	6	16	22	3	7	10
29	–	–	–	1	8	9	2	2	4
30	10	7	17	1	2	3	2	5	7
31	3	2	5	1	9	10	2	4	6
32	–	–	–	2	4	6	3	6	9
33	–	–	–	0	3	3	2	5	7
34	4	2	6	0	5	5	1	3	4
35	–	–	–	1	3	4	0	4	4
36	–	–	–	1	2	3	0	0	0
37	0	0	0	0	2	2	1	3	4
38	1	0	1	0	2	2	0	0	0
39				1	3	4	1	0	1
40				1	3	4	0	0	0
41				0	4	4	1	0	1
42				0	5	5	2	0	2
43				0	4	4	1	3	4
44				0	2	2	2	1	3
45				1	0	1			
46				1	1	2			
47				0	1	1			
48				0	0	0			
49				0	0	0			
50				0	1	1			
Year totals	961	990	1951	2063	2305	4368	1442	1502	2944

that it had remained there for several days. This individual must have emerged between 15 July and 21 August. It can be regarded as an exceptional instance and has not been included in the main body of results. In general, the exuvial collections may be considered to give an accurate indication of the temporal limits of emergence, since searches were made both before, and after, the emergence period each year.

With the single exception quoted above, emergence was restricted to a period of about 40 to 50 days each year and directly followed metamorphosis. The average date for first emergence at the Fish Pond probably lies between 20 and 30 May, since 1951 and 1952 were respectively exceptionally 'late' and 'early' years biologically. In a given area the first date of emergence varies in different habitats

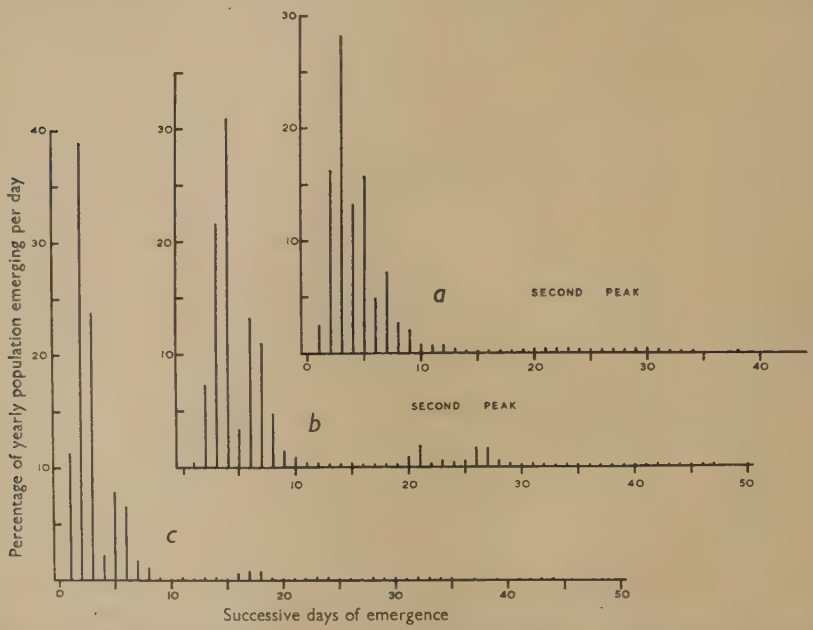

Fig. 12. Time frequency distribution of emergence at the Fish Pond. *a*, 1951 (5 June-12 July); *b*, 1952 (17 May-5 July); *c*, 1953 (25 May-7 July). The dates are the first and last days of emergence.

and must depend largely upon the heat budget in early spring, since adequate food and temperature are prerequisites for metamorphosis (Corbet 1956*a*). The earliest dates upon which exuviae or adults have been recorded before June since 1900 are shown in Fig. 13. The latest emergence recorded during this period was on 23 September 1950 (Longfield, personal communication). In view of the findings described earlier, it is only possible to regard this as an extremely atypical occurrence, caused perhaps by a larva having completed diapause development in the summer. Of *Anax imperator* in Denmark, Wesenberg-Lund (1913) writes that, in a warm summer, many larvae may emerge in July or

August, but no similar observations have been found in the works of other students of this species in Europe. In view of the difficulty of reconciling Wesenberg-Lund's statement with other, better-documented accounts, it is perhaps advisable to regard it as being prompted by an exceptional occurrence, rather than representing a general truth. It is interesting to note that, although the first dates of emergence at the Fish Pond for 1950 to 1953 have a range of 19 days, the last dates differ by 7 days only. This suggests the operation of some seasonally restricted environmental factor which is preventing metamorphosis after a certain date. This possibility is discussed elsewhere (Corbet 1955*a*).

(*b*) *Total numbers*

Yearly populations of adults vary greatly in size. The factors contributing to this variation in a species having a larval duration of two years are doubtless manifold. With so short a series of observations it is not possible to go far towards an explanation of the results. It would be important to know, for example,

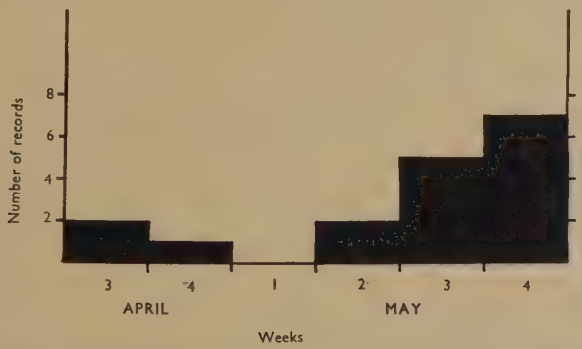

Fig. 13. Distribution of earliest dates upon which exuviae or adults have been recorded before June since 1900 (data from Longfield, personal communication).

whether or not the fluctuations are cyclical. It may be remarked, however (taking into account that the estimate for 1950 is low), that the numbers emerging seem to be a function of the year of emergence rather than that of hatching from the eggs. A heavy mortality amongst final instar larvae after the resumption of activity in spring and before emergence would be consistent with the relationship between dates of first emergence and numbers emerging (see Table 10). The data from marking recoveries support this view. The only marks tested for permanency by trials in captivity were the strips of tin foil. (There were no instances of these being lost during 9 months of activity under crowded laboratory conditions.) Only 45·9% of the 135 larvae released on 31 March 1953 survived to emerge between 25 May and 10 June, 7 to 10 weeks later.

On other counts it seems more likely that adult emergences are dependent more on larval ecology than on the number of eggs laid. Moore (1953) has shown that adult Anisoptera tend to establish a density related to their size and range

of movement-perception when flying over a body of water of given dimensions. This density bears little relationship to the number of mature adults returning to the habitat, and quickly adjusts to a low level after the influx. The equilibrium density of *A. imperator* at the Fish Pond is very low relative to the size of any single year's emergence. It is considered that about 90% of adults usually survive emergence (p. 52), yet the Fish Pond can accommodate a maximum of only 14 mature males at one time. Thus, an abnormally large emergence, apart from intensifying sexual competition, will have a negligible effect on the future, resident, larval population but may be expected to extend the colonization of habitats lying near the limits of the dispersal range.

(*c*) *The emergence curve*

The time-frequency distribution of emergence, referred to as the emergence curve, exhibits a regular and characteristic form. Its pattern is that of a skew curve with an early peak. This indicates the presence of a synchronizing influence late in the larval stage and is clearly correlated with the diapause in the final larval instar (Corbet 1954). This effectively obliterates temporal variation in the time of entry to the final instar, and places the major part of the emergence-group in a position to respond simultaneously to the factors stimulating metamorphosis in spring. It is clear that the mechanization effecting synchronization is competent: larval variation is known to be wide (see Fig. 3*e* and Table 2), yet in 1951, 1952 and 1953, respectively, 92%, 88% and 93% of the annual population emerged within the first 10 days of the emergence period.

There are indications (Fig. 12 *a*, *b*) that the emergence curve is bimodal, having a small, second peak occurring near the 25th day of emergence. This second mode was poorly developed in 1951, containing 5·2% of the annual total, but it became a distinct feature in 1952, when this value rose to 10·6%. (In the calculation of these values the point of division between the two peaks has been chosen as 15/16th days of emergence.) In 1953 it occurred late and was not clearly delimited, but probably contained 3% of the annual emergence. It will be recalled that the existence of two types of metamorphosing larvae was already apparent before emergence. It was considered that the major, earlier, well-synchronized group comprised larvae two seasons old which had undergone diapause in the final instar, whereas the minor, later, dispersed group represented larvae which had entered the final instar in spring and had proceeded directly to metamorphosis. This interpretation was established firmly in 1953 by the results of a marking investigation.

For purposes of this study three types of larvae were considered: (1) Larvae in the final instar on 31 March; such larvae can confidently be assumed to have passed the winter in the final instar. (2) Final instar larvae with a soft cuticle in stage 1 in May; it is very probable, though not certain, that these larvae would have entered the final instar less than a week before capture. (3) Larvae known to have entered the final instar in May. According to the hypothesis advanced above, larvae of type (1) would be expected to emerge during the first peak and larvae of types

(2) and (3) to emerge in the second peak. Accordingly, larvae of these three types were marked with tin foil and records kept of the distribution of recoveries in the emergence curve. All larvae were obtained during routine sampling operations. Those of type (3) were collected in the penultimate instar in April and May, and retained in captivity under natural photoperiods until ecdysis; they were then

Table 11. *Results of larval marking experiment to determine constitution of emergence curve*

Type of larva (see text)	Number marked and released	Number recovered as exuviae	Range of emergence, in days, during 44-day period of emergence
(1)	135	62	1-17
(2)	12	6	26-31
(3)	33	14	25-44

marked and returned to the pond. Recoveries of larvae of type (2) were less informative since the exact date of ecdysis was not known. Details of this marking experiment appear in Table 11 (also MS, F.B.A.). The distribution of recaptures in the emergence curve is shown in Fig. 14. It is quite clear that the results firmly support the interpretation placed upon the two emergence peaks.

Since it is probable that larvae of both kinds are responding to the same environmental factors prompting growth in spring, that is temperature and food (Corbet 1956*a*), it might be expected that the second peak would follow the first

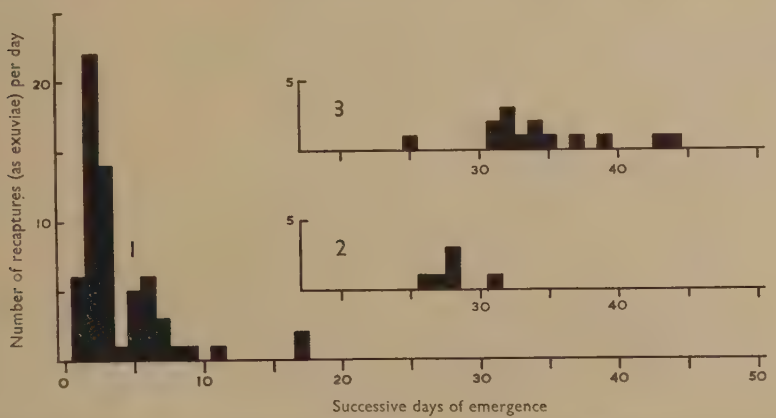

Fig. 14. Distribution of recoveries of marked larvae of 3 types in the emergence period at the Fish Pond, 1953. Larvae which have over-wintered in the final instar (type 1) form the first emergence peak; those entering the final instar in spring (types 2 and 3) emerge later to form the second peak.

by a constant interval. In 1951 and 1952 this was about 25 days. In 1953, however, it was about 32 days, but this year was exceptional in that temperatures fell abruptly on 26 May (the second day of emergence) and remained unseasonably low for two weeks. This doubtless had the effect of delaying and dispersing the second peak.

By virtue of its origin, the second peak is less synchronized than the first, since it is subject to two additional variables: the time at which the final instar is entered, and the time spent in the final instar. The time spent in the final instar (from ecdysis to emergence) by larvae of type (3) averaged 40·6 days but varied from 33 to 51 days. This contrasts strikingly with larvae of the first peak which spend about 9 months in this instar. These results also show that larvae of type (3) complete metamorphosis very much more rapidly than those of type (1). It is not known whether this can be ascribed wholly to higher temperature and perhaps more abundant food later in the season.

The length of time spent in the final instar by larvae of type (3) is significant, since the last dates of emergence are known. If the latest, normal date of emergence is 12 July (1951), then the last date upon which larvae entering the final instar may metamorphose without entering diapause lies about 41 days previously, namely on 2 June. The last date upon which a larva of type (3) moulted (to emerge subsequently in the same year) was 27 May; this individual emerged on 6 July. It may therefore be concluded that larvae entering the final instar in spring, before the end of May, proceed directly to metamorphosis; those doing so later enter diapause and delay metamorphosis until the following spring. This conclusion is of importance for the indication it provides of the environmental factors responsible for the induction of diapause (see Corbet 1956*a*).

(*d*) *Sex ratio*

From analyses of exuvial counts made in 1950 (Corbet 1951) it was concluded that the sex ratio did not differ significantly from unity and that males emerged earlier in the season than females. More extensive data obtained in 1951-53,

Table 12. *Sex ratios and total numbers*

	Sex ratio (males/females)	Males (%)	Total numbers emerging
1950	0·9592	48·96	2071
1951	0·9709	49·26	1951
1952	0·8950	47·23	4368
1953	0·9598	48·98	2944

however, have caused these conclusions to be modified. The sex ratios for the whole annual emergence for the years 1950-53 are given in Table 12. (It must be remembered that exuvial collections were probably discontinued before the end of the emergence period in 1950.) It appears from these data that the true sex ratio (males : females) at emergence is regularly slightly less than unity, being very close to 0·9607 (49% males). The value of 0·8950 (47·23% males) observed in 1952 is probably the result of exceptional circumstances, as will be described below, and therefore an arithmetic mean derived from these data is not likely to be instructive.

The question of whether males emerge before or after females is difficult to

decide owing to wide fluctuations initially and very small numbers at the end of the emergence period. There is little doubt, however, that the conclusions drawn from the 1950 data stand in need of revision. Chi-squared analyses, using similar day-groups, undertaken in the three subsequent years, gave contrary and inconsistent results, suggesting that the range of natural variation in this instance is wider than that accounted for by current statistical theory. Although neither sex appears to emerge earlier in the first emergence peak, there are definite signs of a preponderance of females occurring in the second peak. The disadvantages caused by the small numbers emerging in the second peak can be largely overcome by expressing the results in the form of the cumulative sex ratio to date. In this way it is impossible for a single day's observations in the second peak to cause a major fluctuation in sex ratio. Results plotted in this way are shown in Fig. 15.

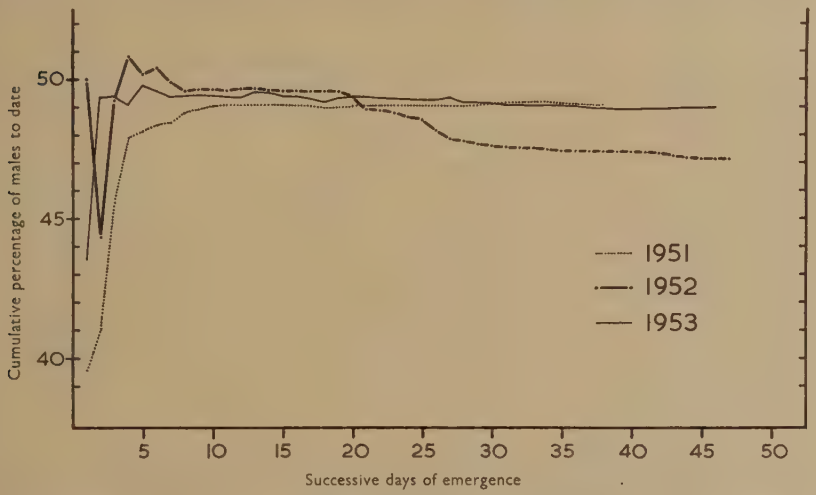

Fig. 15. Cumulative sex ratios during emergence at the Fish Pond in 1951-53. The percentage of males shows a marked drop in the region of the second emergence peak in 1952. The right hand end of each line indicates the total annual percentage of males for the year.

It can be seen that the sex ratio falls abruptly during the main part of the second peak (25th to 27th days of emergence) in 1952. Indeed, in 1952, the second emergence-group, although comprising only 10·6% of the annual total, reduced the gross sex ratio from 0·9802 (49·5% males) to 0·8950 (47·2% males). Thus, the low sex ratio in 1952 can be attributed entirely to the preponderance of females in the second emergence group. A similar trend can be discerned in 1953, although only to a slight extent, but there is no sign of it in 1951, a year when if there is any disparity it is towards a slight preponderance of males in the second peak. In 1951 the second emergence-group was poorly developed.

More data are needed to establish this point, but at present it is reasonable to assume that in years when emergence begins early and the second emergence.group is well represented, the latter is liable to contain a preponderance of females which

will reduce the gross sex ratio. The sex ratio for any given year will thus depend upon the relative development of the two emergence-groups. From the data available, it appears that, when the second emergence-group comprises about 5% of the annual total, probably a usual circumstance at the Fish Pond, the gross sex ratio will be about 0·9607 (49% males), but that in exceptional years when the second peak may comprise 10% of the annual total, the sex ratio may fall as low as 0·8869 (47% males). In examples of the latter type it may be said that males emerge earlier in the season than females.

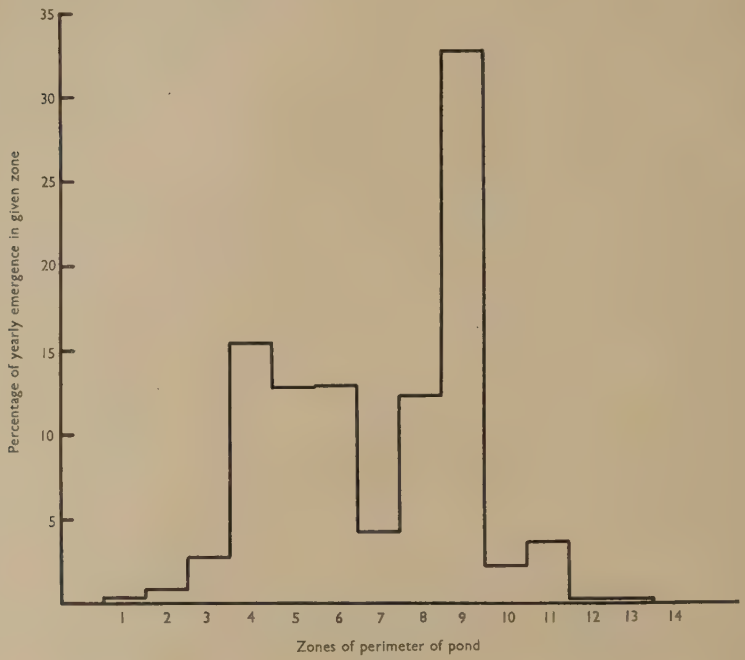

Fig. 16. Differential choice of emergence sites at the Fish Pond, 1953. The zones were defined as follows (see Fig. 1):

Zone 1, Northern margin of *Hypericum* east to B;
" 2, B to mid-point of BC;
" 3, Mid-point of BC to D;
" 4, Oak D (Plate 1 *B*);
" 5, Sallow saplings growing in water by oak D (Plate 3 *C*);
" 6, D to E;
" 7, E to F;
Zone 8, F to south-western sallows, including baffle;
" 9, South-western sallows;
" 10, Zone 9 to H;
" 11, H to northern margin of *Hypericum* north-west;
" 12, Zone 11 to M;
" 13, M to O;
" 14, O to Zone 1.

(*e*) *Emergence sites*

As a sequel to the studies of habitat distribution during larval development and metamorphosis, it is of interest to record the distribution of larvae at the time of emergence. For this purpose, the perimeter of the Fish Pond was divided into

fourteen zones, and the numbers of exuviae collected in each zone recorded separately. The zones are defined and the results given in Fig. 16. Were emerging larvae to swim to the shore and leave the water at random, the density of exuviae in a given region would be a function of the perimeter. Fig. 16 shows that this is not so. Emergence is concentrated in the southern and south-western regions of the pond, within which shaded sites receive preference. Thus zone 8 (the baffle) was better patronized than zone 7 (the open path along the dam, representing a comparable sector of the perimeter) to an extent of 363 to 124, although neither zone possessed submerged sticks encouraging pre-emergence aggregation. An interesting example of the extent to which the distribution of aquatic plants determines the choice of emergence sites is afforded by a comparison of emergence in 1950 and 1953. In 1950 (see Corbet 1951) substantial emergence occurred on a thick stand of *Alisma plantago-aquatica* L. in region B between the *Hypericum* mats. In the three subsequent years there were never more than one or two emergent leaves of *Alisma* in this region, although there were signs of a recrudescence of this plant in 1953, and the emergence there was negligible.

(*f*) *Diurnal rhythm*

Study of the diurnal rhythm of emergence has relevance to the validity of exuvial collections as representing day-groups during the emergence period. No special study has been made hitherto of diurnal rhythm of emergence in Odonata, although it has often been stated (e.g. Tillyard 1917) that most species emerge at dawn. Recent observations suggest, however, that such a generalization may be more applicable to observers than to dragonflies, and that where temperature is not a limiting factor most Odonata that do not do so during the day-time emerge at dusk and fly at dawn. Rhythmic emergence is a widespread phenomenon in insects and has been demonstrated in many groups (Wigglesworth 1950). Members of the Aeshnidae have previously been observed to emerge between dusk and dawn (East 1900, Wilson 1920, Lucas 1930, Straub 1943), and observations at the Fish Pond have confirmed that *Anax imperator* is typical in this respect.

In order to obtain an objective expression of the diurnal rhythm, a series of arbitrary, well-defined stages in the process of emergence was established; then restricted groups of larvae were assigned to these categories on successive occasions during emergence. Three main stages were defined: (1) Larva completely out of water but cuticle not split: (*a*) locomotion by jet propulsion if returned to the water; (*b*) locomotion not by jet propulsion but by convulsive, lateral movements of the abdomen as exhibited by larvae of the Zygoptera. (2) Cuticle of thorax split (this includes the inverted 'resting stage'), the abdomen remaining in the exuvia. (3) Abdomen withdrawn from exuvia, the body supported by legs alone; in this stage the wings and abdomen reach their full size. These stages are illustrated in Plate 2.

The sampling region selected for making counts was the group of sallow saplings with submerged roots growing near oak D (see Plate 3 *C*). This comprised zone 5 of the perimeter of the pond (Fig. 16) and accommodated about 13% of the total

larvae emerging. Apart from its representative qualities, it was a convenient site for nocturnal observation. Control counts made in other regions of the pond indicated that the sampling zone was typical in all important respects.

The results of an emergence count made on 23 May are shown in Fig. 17 (also MS, F.B.A.). It is clear that most larvae leave the water at about 2145 B.S.T. and remain in stage 1 for three-quarters of an hour. Stages 2 and 3 are entered with similar regularity, stage 2 lasting about an hour. After entering stage 3 first the wings and then the abdomen expand rapidly, so that within an hour, at about 0030, adults are fully formed. They remain with the wings closed until about 0345, when these are abruptly opened. The maiden flight, which occurs at about 0430, is even more closely synchronized than the emergence of the previous night (Fig. 17, 4).

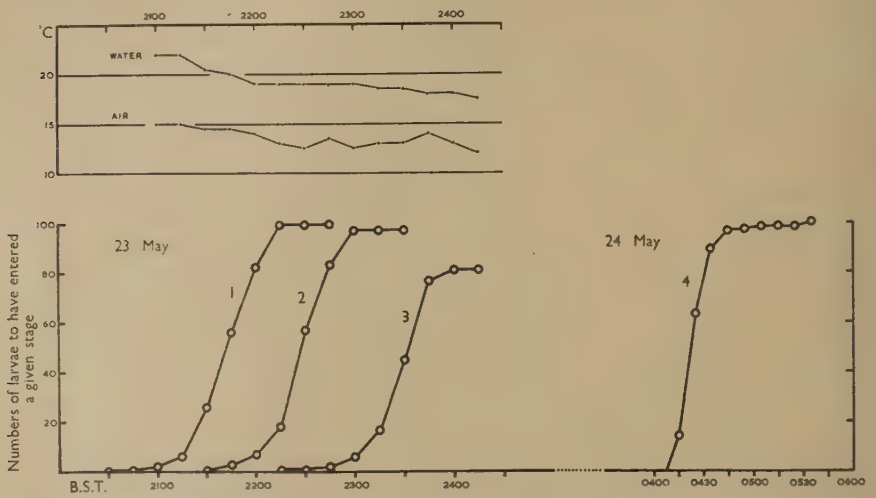

Fig. 17. Normal diurnal rhythm of emergence illustrated by counts of emerging larvae made at the Fish Pond, May 1952. The successive stages of emergence are illustrated in Plate 2.

Asymptotic values of stages 1-3 differ owing to mortality during emergence. Stage 4 represents the maiden flight; to obtain these records a different sampling region was used. Dawn flight is more closely synchronized than evening emergence.

(g) *Divided emergence*

Confirmation of the pattern of normal daily emergence vindicates fully the use of morning exuvial collections as indices of the previous night's emergence. Occasionally, however, emergence occurs during the day-time. This phenomenon may be termed 'divided emergence'. On occasions when day-time emergence has been observed, there have always been numbers of untenanted exuviae *in situ*, indicating that an emergence also occurred the previous night. A circumstantial correlation has been noticed between divided emergences and cold nights. Considerable light was thrown on the status of divided emergence in the normal rhythm by results of counts made on 20 May 1952 (Fig. 18 and MS, F.B.A.). On this night air temperatures fell rapidly during the time normally occupied by

stage 1. Larvae spent longer than usual in stage 1 (at least one hour, instead of three-quarters of an hour) and entered stage 2 increasingly slowly as the night progressed. After 0015 no further individuals entered stage 2, although only 50% of the emergence group had already done so. Individuals in stage 2 entered stage 3 normally. The remainder stayed motionless on the emergence supports until about 0130, when they began irregularly to return to the water; eighteen such larvae were given identification marks with cellulose paint as they entered the water. Counts made the following morning, when a day-time emergence occurred, indicated that a group of larvae left the water between 0900 and 1000 and emerged shortly afterwards. All of the sixteen recoveries of larvae marked the previous night were obtained during this morning emergence.

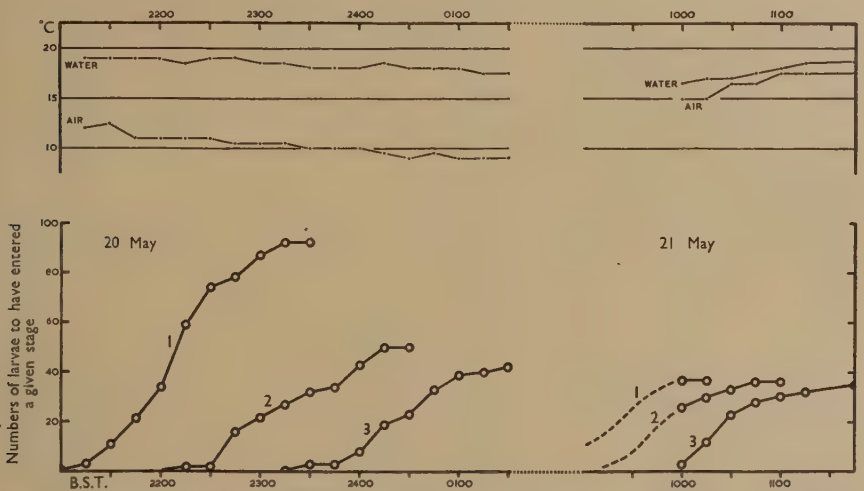

Fig. 18. Divided emergence, illustrated by counts of emerging larvae made at the Fish Pond, May 1952. Asymptotic values of stages 1 and 2 differ owing to the return of about 40 larvae to the water at 0130; those of stages 2 and 3 differ owing to mortality. The larvae which had returned to the water emerged between 0900 and 1000 the next morning, presumably when the air temperature was no longer too low for emergence to occur.

An environmental factor showing a wide difference on the two nights of observation is air temperature (compare Figs. 17 and 18). On the night of 20-21 May no further larvae entered stage 2 after the air temperature fell below 10° C; instead they returned to the water and emerged the following morning when air temperatures had risen. A point of significance is that they were unable to delay emergence until the following evening. This suggests that they had taken an irrevocable physiological step which rendered emergence urgent. Unlike larvae emerging in the evening which swim to emergence supports by jet propulsion (method 1 (*a*), p. 43), those doing so during the day usually swim by lateral movement of the abdomen (method 1 (*b*), p. 43). This was demonstrated by a small experiment carried out on 28 May 1953. On this day, many larvae were leaving the water between 0900 and 1000, forming the second part of a divided emergence. Ten

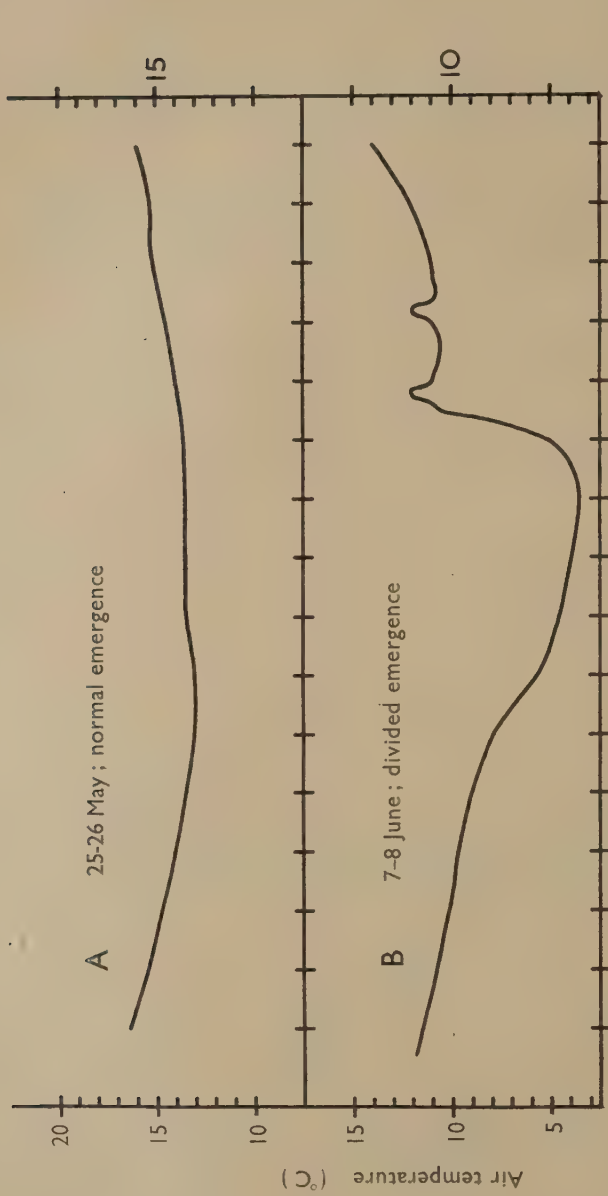

Fig. 19. Thermograph tracings taken near oak D at the Fish Pond 1953. The discontinuous rise in temperature on 8 June is thought to have been caused by the sun passing a clump of trees.

larvae (five males and five females) were lifted off their emergence supports immediately before the tip of the abdomen left the water; they were then placed in the water some distance from an accessible support. Of these larvae eight (four males and four females) swam by method 1 (*b*) after the manner of Zygoptera, and the remainder did so by method 1 (*a*) using jet propulsion very weakly. It is well known that the respiration of Anisoptera changes abruptly from rectal to spiracular at emergence (Müller 1924). It is therefore suggested that a day-time emergence comprises larvae of the previous evening's emergence-group which having entered stage 1 (*b*) encountered an air temperature below the threshold permitting entry to stage 2. Since this involved a change of respiration, emergence could be postponed only as long as temperatures remained unfavourable. It is possible that some larvae may experience prohibitive temperatures while still in stage 1(*a*). These presumably are capable of postponing emergence for 24 hours. This may influence daily fluctuations in emergence rate.

In 1953, during the unusually cold weather which followed the beginning of emergence, divided emergences were the rule rather than the exception. Air temperatures at the Fish Pond upon nights in 1953, when there were normal and divided emergences respectively, are compared in Fig. 19. These observations upon the diurnal rhythm of emergence demonstrate that, to obtain day-classes during the emergence period, it is justifiable to combine morning collections with those of the night before.

(*h*) *Mortality during emergence*

Three major types of mortality during emergence have been identified: (i) Incomplete ecdysis; (ii) incomplete expansion of the wings, so as to prevent flight; (iii) predation by birds before flight.

(i) The incidence of mortality due to incomplete ecdysis can be measured by recording the number of individuals still remaining in half-opened exuviae on the day after an emergence. It appears that incomplete ecdysis may be due either to the inability of an isolated individual to moult, or to the effects of overcrowding on desirable emergence supports. The very low incidence of incomplete ecdysis over a considerable period when daily emergences are small indicates that individual incompetence is seldom the cause. The effect of overcrowding is shown in Plate 3 *B*; it is clear from Table 13 that this factor is chiefly responsible for this type of mortality during emergence. Incomplete ecdysis is a phenomenon limited almost entirely, and to a disproportionate extent, to the first emergence peak. On the modal night (1953) it can account for a loss of 2·4% of the day-group.

(ii) Adults which have left their exuviae but suffered mishap when expanding the wings can be found after dawn, either clinging to an emergence support or often struggling in the water. This type of crippling is nearly always the result of physical interference either by the agency of wind or by later emergers mutilating the delicate wing-sheaths with their tarsal claws. Anything at this critical stage which knocks an adult into the water or causes its wings to touch a rough object, is liable to prevent it from being able to fly the following morning. The

density-dependence of this type of mortality is even more obvious than for incomplete ecdysis; thus, as much as 16% of a daily emergence-group can perish in this way (see Table 13, 1953). Loss over the whole emergence period due to incomplete expansion of the wings was higher by far in 1953 than in 1952. Low nocturnal temperatures and cold winds on the nights of 26 and 27 May are thought to have been principally responsible for this disparity.

On several occasions in 1952 when noctural emergence counts were being made, individuals of the Great Crested Newt, *Triturus c. cristatus* (Laurenti), were seen congregating just beneath the surface in the region of the sallow saplings (Plate 3 *C*). If a teneral adult of *Anax imperator* fell into the water in this region, it

Table 13. *Counts of dismembered wings, crippled exuviae and deformed adults on successive days of emergence at the Fish Pond, 1952 and 1953*

Daily counts of wings have been classified according to the methods (1), (2), and (3) mentioned in the text. L, left; R, right; F, forewing; H, hind wing.

	(1)				(2)				(3)								
	L		R		L		R		L		R		Day minima			Cripples	
Day of emergence	F	H	F	H	F	H	F	H	F	H	F	H	(1)	(2)	(3)	Exuviae	Adults
1952																	
2	1	2	1	1	1	2	1	1	1	2	1	1	2	2	2	4	–
3	16	15	18	16	18	17	19	16	14	14	15	15	18	19	15	3	18
4	7	4	2	11	7	4	2	11	7	3	2	9	11	11	9	21	107
5	17	22	22	24	17	24	22	26	16	20	22	20	24	26	22	3	4
6	36	40	28	43	38	43	29	46	35	38	25	35	43	46	38	6	26
7	10	9	5	10	10	9	5	10	10	8	5	9	10	10	10	7	20
8	5	7	5	5	5	7	5	5	4	7	5	4	7	7	7	2	1
9	6	5	4	4	6	5	4	4	3	5	4	4	6	6	5	1	–
10	3	3	5	4	3	3	5	4	3	3	5	2	5	5	5	1	1
11	1	1	3	3	1	1	3	3	1	1	2	3	3	3	3	–	–
12	–	2	1	–	–	2	1	–	–	1	1	–	2	2	1	–	–
13	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
14	1	1	–	–	1	1	–	–	1	1	–	–	1	1	1	1	–
15	1	1	–	–	1	1	–	–	1	1	–	–	1	1	1	2	–
16	–	1	–	–	–	1	–	–	–	–	–	–	1	1	–	–	–
17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
20	1	–	1	–	1	–	1	–	1	–	1	–	1	1	1	–	–
21	9	15	13	16	9	15	13	20	9	14	12	15	16	20	15	–	–
22	1	–	–	–	1	–	–	–	1	–	–	–	1	1	1	–	–
23	3	5	5	4	3	5	5	4	3	5	5	4	5	5	5	–	–
24	2	1	2	1	2	1	2	1	2	1	2	1	2	2	2	–	–
25	1	3	2	2	1	3	2	2	1	3	2	1	3	3	3	–	–
26	8	4	9	8	9	4	10	8	8	4	8	8	9	10	8	–	–
28	1	2	–	1	1	2	–	1	1	–	–	1	2	2	1	–	–
35	1	1	2	–	1	1	2	–	1	1	2	–	2	2	2	–	–
36	–	1	–	–	–	1	–	1	–	1	–	1	1	1	1	–	–
38	1	–	–	–	1	–	–	–	1	–	–	–	1	1	1	–	–
41	1	1	1	–	1	1	1	–	–	–	1	–	1	1	1	–	–
Totals	133	146	129	154	138	153	132	163	124	133	120	133	179	189	160	52	177

TABLE 13 (continued)

Day of emergence	(1) L F	(1) L H	(1) R F	(1) R H	(2) L F	(2) L H	(2) R F	(2) R H	(3) L F	(3) L H	(3) R F	(3) R H	Day minima (1)	Day minima (2)	Day minima (3)	Cripples Exuviae	Cripples Adults
1953																	
1	6	8	5	3	6	9	5	3	6	8	5	2	8	9	8	–	2
2	8	8	12	11	8	9	12	11	8	8	12	10	12	12	12	27	138
3	36	33	37	42	36	37	41	49	36	29	55	41	42	49	41	16	112
4	22	33	28	25	24	37	29	29	22	29	25	23	33	37	29	2	4
5	12	19	12	16	14	20	14	17	12	18	12	13	19	20	18	1	–
6	44	51	43	43	46	55	45	48	43	36	38	38	51	55	43	5	2
7	7	9	15	10	8	10	16	11	6	7	11	10	15	16	11	–	4
8	4	4	4	3	4	5	4	4	4	3	2	3	4	5	4	2	1
9	3	1	1	1	3	1	1	1	3	1	1	1	3	3	3	–	–
11	–	1	1	2	–	1	1	2	–	1	1	2	2	2	2	–	–
12	1	1	–	1	1	1	–	1	1	1	–	1	1	1	1	–	–
13	1	2	1	–	1	2	1	–	1	1	1	–	2	2	1	–	–
14	–	–	1	–	–	–	1	–	–	–	1	–	1	1	1	–	–
15	2	–	–	–	2	–	–	–	1	–	–	–	2	2	1	–	–
16	–	2	2	2	–	2	2	2	–	2	2	2	2	2	2	–	–
17	–	1	1	–	–	1	1	–	–	1	–	–	1	1	1	–	–
18	1	–	–	–	1	–	–	–	1	–	–	–	1	1	1	1	–
30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Totals	147	173	163	159	154	190	173	178	144	145	146	146	199	218	179	55	263

quickly attracted the attention of the newts, one of which would usually ingest the whole or part of the insect's abdomen. The thorax, head and wings were commonly shaken free and left floating on the surface. Adults recorded in this category were often found in this condition. It is possible that a few such individuals may have become waterlogged and sunk before morning, and this would have meant that the routine count would have been an underestimate. Occasionally an adult knocked into the water is able to climb out and dry its wings sufficiently to enable it to fly at dawn the next day. The attendance of newts would tend to reduce this possibility, and thus perhaps cause a greater number to be recorded in this category than would have been in their absence.

(iii) The incidence of bird predation at this habitat has been referred to previously (Corbet 1951). Almost all the mortality due to bird predation from 1951 to 1953 can be ascribed to the activities of a pair of blackbirds (*Turdus m. merula* L.) nesting on the dam at the Fish Pond. Only one pair of birds was involved each year but it is not known whether the same individuals were represented in both years. The positions of the nests of the pairs that defended the Fish Pond as their territory are shown in Fig. 1. A brood was reared in each nest in 1952 and 1953. In 1953 the young birds left the nest on 5 June, the 12th day of emergence. The adults remained, however, and continued to prey to a slight extent on emerging dragonflies.

During emergence, blackbirds were observed to eat dragonflies in two ways.

At dusk, when some larvae were making their way to the shore, clambering through debris in shallow water, a bird would hover over them and pick them up with its feet. The larva shown in Plate 3 *A* was in a position in which many larvae were taken; it was struggling through a surface scum of sallow catkins which carpeted the water at the southern end in late May 1953. This larva was near oak D. After being captured, a larva was usually battered to death on a nearby patch of bare ground and then taken away to the nest. On account of this procedure, no evidence of predation remained afterwards. Therefore the extent of this cause of mortality has not been measured. The time each day when this source of food was available was very short, however, on account of the usual postponement of larval activity until after dark. Therefore it is not thought to have been a substantial item.

In the morning, shortly after the dawn flight, predation of teneral adults remaining on emergence supports was liable to be heavy. Both birds would begin feeding at about 0430 B.S.T. Hovering by an emergence support a bird would remove a teneral adult, take it to a bare, hard patch of ground or 'anvil', and then remove the wings. The body of the dragonfly would then be eaten or taken to the nest. The result of this procedure was that the dismembered wings of consumed adults remained on the anvils. The sites of these anvils were determined in 1951, and in the following two years collections of dismembered wings were made daily during the emergence period. Attempts were made by searching the whole region to make collections exhaustive, but it is clear that they fell short of this ideal. The results obtained, however, do allow some conclusions to be reached as to the minimum amount of predation occurring during those years.

In the Anisoptera if more than the distal fifth of a wing is available it can be identified as a fore- or hind-wing. Furthermore, owing to the convex and concave tracheation, even a small fragment can be recognized as belonging to a right or left wing. Thus wing fragments could in all save a very few instances be assigned with confidence to one of four categories. Such a method of recording provided more information than could have been derived from totals of unclassified wings. Since only about two-thirds of the wings were collected in an entire condition, daily collections of wings could be recorded in three ways: by the minimum number of whole wings which could be obtained from a day-group by fitting together tips and bases; by the maximum number of wings which could have provided the given fragments, each fragment being considered to be representative of a separate wing; or by the total number of pterostigmata present. In the last, as in the first, it is impossible to record a whole wing more than once, but this method may be expected to provide a lower value per day, since bases without tips to represent them will not be recorded. Since, however, fragments of the same wing may be collected on different days, the third is the most accurate method of recording minimum total wings for the whole season.

Data for daily collections, recorded in these three ways, appear in Table 13. The term 'day minimum' represents the minimum number of adults which could have provided a given daily wing-count, i.e. the minimum number of insects for

the maximum number of whole wings. If counts for right, left, fore- and hind-wings differ on a given day this may be due to incomplete collection of wings on that day, or to inclusion of wings missed on previous days. In either or both of these cases, it is clear that the sum of the day minima must exceed any of the sums of the four classes of wings. The sum of day minima can equal, exceed, but never fall short of sums for the several wings (see totals at foot of Table 13).

It is instructive to determine the relationship between sums of day minima and sums of individual wing-counts, for this will provide an expression of the variation in results due to both causes. Let the sum of day minima be denoted by Σd. Then Σd for method (1) in 1952 is 179. Also, let the sums for the four wings be indicated by Σx_1, Σx_2, etc. For method (1) in 1952 these values are 133, 146, 129 and 154. Let Σx be the highest (and therefore operative) value of Σx_1, Σx_2, etc., and let r denote the number of days or horizontal rows. Then, the excess of Σd over Σx will be dependent upon the distribution of counts for one wing upon successive days (i.e. inequality of values reading vertically), the distribution of

Table 14. *Mortality during emergence, as estimated by counts of dismembered wings*

	Values of $\Sigma d/\Sigma x$	
	1952	1953
Method (1)	1·155	1·150
(2)	1·160	1·147
(3)	1·202	1·226

counts for all wings on any single day (i.e. inequality of values reading horizontally), and the average daily number of wings (i.e. the excess of Σx over r). To obtain a maximum value for Σd given Σx and r the day counts must be distributed so that a maximum count is given every day. Clearly the most effective distribution towards this end is for any day to contain values for one of the four wings only; then every wing will register to its full value. Obviously this value of Σd cannot be exceeded.

For method (3), in 1952, the maximum possible value of Σd is $\Sigma(x_1+x_2+x_3+x_4) = 124+133+120+133 = 510$. If we consider the values of 120 and 124 for the fore-wings as incomplete, the maximum value of $\Sigma d = 4\times133 = 532$. The minimum value of Σd in 1952 is obviously 133.

An approximate measure of the errors inherent in each method due to incomplete collection upon separate days can be obtained by calculating $\Sigma d/\Sigma x$. These values are given in Table 14. The close correspondence of these values in 1952 and 1953 indicates that the errors in each of the three methods are likely to remain fairly constant from year to year. Since values of $\Sigma d/\Sigma x$ have a possible theoretical range from 1 to 4, it is clear that there has not been serious distortion of day minima by incomplete collecting. It seems, therefore, that an estimate of the order of the yearly predation by birds during emergence can be obtained from values of Σx. Using the formula $(\Sigma x\times100)/(\text{total annual emergence})$ to provide

an estimate of the percentage killed by birds we obtain the values in Table 15.

It can be assumed with confidence that predation by birds during emergence was at least 3% of the annual population in 1952, and at least 5% in 1953. Minimum values for mortality during emergence, from the three sources of information available, have been itemized in Table 16. On the basis of these figures, it is not unreasonable to assume that about 90% of the yearly population of adults survived emergence in 1952 and about 83% in 1953.

Table 15. *Minimum percentage mortality during emergence, as estimated by counts of dismembered wings*

	1952	1953
Method (1)	3·5	5·9
(2)	3·7	6·5
(3)	3·0	5·0

Mortality is restricted almost entirely to the first peak of the emergence curve. In 1953 it was higher in all classes than in 1952 but especially that due to incomplete expansion of the wings. As mentioned earlier, a spell of unseasonably cold weather, which coincided with the main peak of emergence in 1953 and obliged many adults to emerge during the day-time, often in a stiff breeze, is probably chiefly responsible for the excessive number of adults failing to achieve complete expansion of the wings. Mortality due to incomplete ecdysis may be expected to show a fairly constant density-dependence for a given habitat, since it is conditioned by the degree of competition for emergence supports (see Plate 3*B*). The increased mortality in 1953 may reasonably be attributed to the closer synchronization. It is worthy of note that in both years maximum mortality occurred on

Table 16. *Minimum percentage mortality during emergence due to three causes*

	1952	1953
(1) Incomplete ecdysis	1·2	1·9
(2) Incomplete expansion of wings	4·3	8·9
(3) Predation by birds	3·0	5·0
Totals	8·5	15·8

the modal nights. That the predation by birds would increase substantially in a year when the normal rhythms of emergence and dawn flight were upset is to be expected. Yet it must be remembered that many more adults emerged in 1952 than in 1953 (4368 against 2944), and therefore percentage figures for mortality tend to be misleading. Actually (using method (3)), 133 adults were eaten in 1952 and 146 in 1953, a very small difference. It is remarkable that the disparity between 1952 and 1953 for this item is not greater, and it may be that the predators in this case (who held the monopoly of the food supply by successful defence of territory) were approaching their asymptotic capacity with respect to this

particular kind of food. Lack (1954) cites examples of a similar type in which birds have been found to take a constant number of a prey species showing annual variation in density.

The above analyses suggest that mortality during emergence was increased substantially in 1953 and that this increase was causally related to the unusually severe weather conditions. It is probably reasonable to regard 10% as an average figure for mortality during emergence at the Fish Pond.

(*i*) *Discussion*

A feature of the normal emergence rhythm which could be turned to profitable account in quantitative studies of adult ecology is the protracted duration of stage 3. Between 0100 and 0300 each night during the emergence period, all the newly emerged adults are immobile on the emergence supports. Large-scale marking at this time would permit the exact age of all recaptures to be known, a rare achievement in population studies. Since the strong flight and power of dispersal of Anisoptera prohibit extensive marking during adult life this method would provide information at present unobtainable by other means. Furthermore it is usual for newly emerged adults to remain upon or close to their own exuviae until the maiden flight. Thus it would be possible to follow the behaviour of an individual from the larval to the adult stage. This gap is seldom bridged in autecological studies, but to do so would probably prove instructive. It might, for example, contribute to a better understanding of adult density regulation and sexual behaviour by determining whether individuals from the second emergence group behave in a manner similar to those from the first. The practicability of this method was tested on the night of 6-7 June 1951, when ten newly emerged adults were marked on the legs with cellulose paint shortly before first flight. One of these, a female, was recaptured while hawking strongly over the common behind G on 10 June.

The adaptive value of nocturnal emergence is obvious in the case of large species requiring some hours to transform, occurring at high density, having a synchronized seasonal emergence, and being subject to predation by birds. It may be that nocturnal emergence is the more general condition amongst Odonata, but that in temperate climates, where night temperatures may be below the threshold for transformation or flight, some species have become adapted to emerge in the day-time. The phenomenon of divided emergence in *Anax imperator* suggests an evolutionary step by which day-time emergence might have become established. Divided emergence seems to be a physiological necessity imposed by low air temperatures obtaining after stage 1(*b*) has been reached. The adaptive significance of such a response, if any, may not refer solely to the temperature at which emergence is possible. For instance emergence may be completed successfully at a temperature below that which evokes its postponement. If low evening and dawn temperatures are correlated, then divided emergence may be an adaptation to prevent a day-group of emerging adults from being stranded, unable to fly, at dawn, when predation by birds is liable to be heaviest. Divided emergence may

postpone the appearance of adults to a time when predation is less severe (intensity of attacks by birds seems greatest at dawn) and when transformation can proceed more rapidly.

ADULT LIFE

Very little succinct information exists on the ecology of adult Anisoptera, a situation that can perhaps be ascribed to their wide range of dispersal and to the difficulty of capturing specimens. The recent work of Moore (1952*a*, 1952*b*, 1953) has contributed greatly towards a systematic interpretation of sexual behaviour in adult dragonflies. Observations upon *A. imperator* recorded in this section are necessarily incomplete, since the writer was obliged to leave the Fish Pond in late July each year. This meant that, at the most, only the the first 8 weeks of the flying season could be observed. Nevertheless, an approximate idea of the pattern of adult life can be obtained from observations made at this habitat from 1950 to 1953.

(*a*) *The maiden flight*

Newly emerged adults fly at dawn (see Fig. 17). About an hour before sunrise the wings are opened abruptly and, shortly afterwards, if the air temperature is high enough, they begin to vibrate. This produces an audible rustling, which at the Fish Pond used to commence at about the time that the last bat left the pond, the nightjars stopped churring, and it first became possible to read without the aid of a torch. Activity and vibration of the wings increase in intensity until, about 40 min before sunrise, the first adult takes to flight. Sotavolta (1954) has demonstrated the importance of wing-whirring as a means for raising the thoracic temperature of insects above that of the environment. The protracted period (20 min) of wing-vibration preceding maiden flight may be regarded as an indication that the ambient temperature at dawn is well below the threshold for flight.

When about to fly, dragonflies climb up their emergence supports, meanwhile increasing the wing-stroke frequency until they become airborne. As a rule adults begin the maiden flight by rising slowly, often working their way through a canopy of overhanging branches, until about 3 m above any obstacles impeding the view; they then fly away rapidly in a well-defined direction. In some individuals, the abdomen is still so soft that it cannot be held horizontally, but instead hangs downwards during flight.

For the maiden flight, it appears that adults orientate so as to fly away from water. Observations made at oak D on 23 May 1952 showed that of 123 dragonflies making successful flights 102 left the pond to the south, 16 to the west, 5 to the east and 0 to the north. To record these results the compass was divided into quadrants. This matter was investigated experimentally on 30 May 1953. Five stations were set up in the positions shown in Fig. 20, four being placed around the perimeter of the pond and the fifth at a point on the common south of F (see Fig. 1), out of sight of water. This fifth station was situated in an open patch of heather. Between 0235 and 0325 B.S.T. on 30 May (sunrise on this date was at 0450) newly formed adults were transferred from the south-west corner of the

pond, where they had emerged, to each of these stations. This procedure was adopted to check the possibility that orientation might have been determined in the larval stage during the journey to the emergence supports. A small trellis-frame of sticks was erected at the water's edge at each of stations 1 to 4 and also at station 5. The dragonflies were placed on these frames, all being in position by 0330. Observers stationed by the frames recorded the direction of flight after the preliminary orientation had taken place. The direction recorded was that taken for the first, straight, horizontal, rapid flight. Care was taken to avoid influencing the direction of flight by sudden movements on the part of the observer. From the results (Fig. 20) it can be seen that adults usually orientate so as

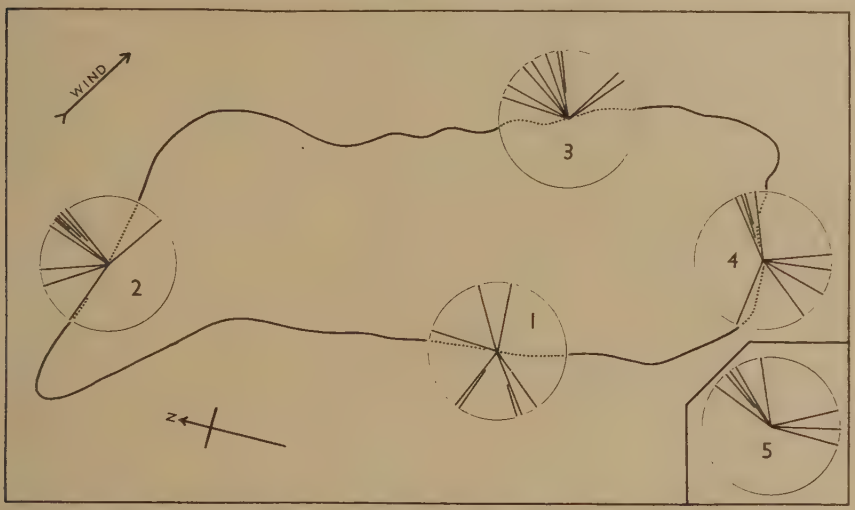

Fig. 20. Flight orientation experiment at the Fish Pond, 30 May 1953; plan of pond to show positions of release stations.

Teneral adults were transferred from the south-west corner of the pond, where they had emerged, to the stations 1-5 before dawn. The directions of successful maiden flights from these positions are shown as radii in the circles. It is possible that some of the flights of adults leaving station 4 were influenced by the positions of large obstructions, such as oak D, which would have provided substantial barriers to flight and vision. Station 5 was about 40 metres south of the pond, out of sight of water.

to fly away from water. This seems to represent a type of telotaxis (Wigglesworth 1950), but the critical properties possessed by bodies of water which evoke this response are not known. Perhaps orientation may be determined visually with regard to the presence of a plain reflecting surface. This orientation away from water for the maiden flight may be an important adaptation towards prevention of mortality amongst teneral adults due to sexual aggression from mature males.

The length of the first flight may vary from about 20 m to a distance greatly exceeding 200 m. The distance flown may perhaps be determined by fatigue, since flights seem to be shorter on colder mornings. Adults have been seen to alight on pine and oak trees, from 1 to 10 m above the ground, and on clumps of heather. They usually leave these positions later in the day. Only two out of

seven adults watched on 30 May 1953 still remained at the first places of rest at 1500 on the day of first flight, and these had both left by 1700.

(*b*) *The maturation period*

For at least the first week after emergence, beginning on the first fine warm day, adults fly strongly over the common away from water. During this period both sexes can be seen hawking over and settling low amongst the heather near the pine trees about 100 m south-west of the pond; the dragonflies appear teneral, feed actively, and show no sexual response to adults of either sex. They also appear to retain their negative taxis to water. Gonads of one-day-old adults are in an undeveloped state, and it is assumed that during the period spent away from water adults attain sexual maturity. A similar terrestrial phase has been found a prerequisite for mature adult flight in *Argia* (Borror 1934), *Pyrrhosoma* (Corbet 1952) and *Lestes* (Corbet 1956*b*). It is probably a general feature of the life-history in Odonata, and is doubtless of significance in effecting dispersal.

One of the first indications of the return to water is provided by males making flights of a few minutes' duration over the pond. As shown in Table 17, this

Table 17. *Maturation and adult life at the Fish Pond*

	1951	1952	1953	Averages
Emergence began	5 June	17 May	25 May	
First male seen over water (days after emergence)	7	8	12	9·0
First sexual behaviour seen over water	11	9	14	11·3
First female seen ovipositing	13	16	16	15·0
First blue female seen	27	32	>41	>30

behaviour begins about 1 week after emergence, by which time males have assumed the mature coloration. It is typical of such males to stray from their feeding beats on the common nearby, fly to and fro over the pond for a minute or two, and then return to their previous positions. After the ninth day of adult life, males begin to exhibit sexual behaviour over water. In 1953, when air temperatures were exceptionally low during the first 2 weeks of the emergence period, this stage was not reached until the 14th day. About 2 or 3 days after arrival of the first sexually mature males, females return to the water to oviposit. In order that the maximum number of females shall be fertilized, it is clearly desirable that males shall already have established themselves at the aquatic habitat before the females arrive there. In *Anax imperator* it can be seen that this is achieved by the more rapid maturation of the males, and not, as was previously thought (Corbet 1951), by their earlier emergence.

(*c*) *The reproductive period*

Mature males quickly establish beats over the water; these beats are analogous, but not homologous, to the territories of birds (see Moore 1952*a*). Upon the arrival of a female, copulation occurs promptly, the pair usually flying a short distance *in copula* (rarely *per collum*) and then alighting on vegetation near the

pond. After copulation females oviposit without delay and then leave the pond. On no occasion was a female observed ovipositing with a male in the tandem position. Only once were two adults seen flying over the water *per collum*, and this was during an interrupted copulation. However, Münchberg (1932) records post-copulation tandem flight as not uncommon in *A. parthenope* Sélys. It seems almost certain that females return later to oviposit again, but it is not known how frequently they mate. Observations made by Moore (personal communication) suggest that most oviposition visits are not immediately preceded by copulation. Thus, it seems likely that the effects of a single mating may last for several days. In 1951 a female was seen ovipositing 20 days after the last emergence. Assuming this individual to have been a resident, this would have been about 7 days after her first return to water as a mature adult. Possibly when a female with a mature batch of eggs mates but separates prematurely, she will copulate immediately after oviposition. A female disturbed from low littoral weed, and almost certainly from oviposition, was picked up by and seen to copulate with a male on 1 July 1952.

The green colour of the female abdomen harmonizes closely with the *Potamogeton*, amongst which most of the oviposition at the Fish Pond takes place. This probably does much to protect females from untimely male interference, as must also their habit of continuing oviposition during overcast weather or light rain, when few males are over water. During oviposition, females may remain at a single site for 10 min but usually they move frequently, seldom spending more than 30 sec in one spot. It is usually during the short flights between sites that ovipositing females attract the sexual attentions of males. Females exhibit a characteristic behaviour pattern if males flying overhead attempt to grasp them: first, the abdomen is flexed ventrally in flight; then, if interference continues, the female rises, revolving rapidly about a vertical axis. A similar 'escape' reaction has been observed in some Coenagriidae. It may be that such a behaviour pattern achieves a lowering of the mating stimulus by representing an exaggerated oviposition posture. Moore (1952*b*) has shown that in the Libellulidae ovipositing females do not provide the necessary stimulus for copulation. In *Anax imperator*, this behaviour usually relieves the female of male interference, but if it fails to do so the female will attempt to rise above the male.

The impressions on the postero-dorsal surface of the female compound eyes, made by the male inferior appendage during assumption of the tandem position, can be used as a means for determining by inspection whether or not a given female has mated (Fig. 21). In theory, it is conceivable that a female might have been grasped but released before copulation could take place. In practice, however, such an event must be so infrequent as to have a negligible effect upon the validity of the method. That similar marks are not infrequently found on males indicates that inter-male copulation is sometimes attempted. This is in accord with Moore's findings (1952*a*) that males are often unable to distinguish the sexes of their own species. Males are apparently able to copulate more than once. A male possessing eye-marks caught on 3 June 1952 while *in copula* was observed to

mate with a different female 30 min later. (Conspicuous paint marks on the wings enabled individuals to be recognized.)

It is not known how long mature adults live, but the few recaptures obtained from releases of marked specimens show that males can survive for at least 26 days after completion of the maturation period. One consequence of the closely synchronized emergence exhibited by spring species is that maximum adult life-span forms a high proportion of the flying season. In a population of *Pyrrhosoma nymphula* studied at the Fish Pond in 1951 (Corbet 1952), the ratio (flying season) : (post-maturation maximum life-span) was about 1·6. The end of the flying season for *Anax imperator* at the Fish Pond is not known, but records obtained from visits in late summer indicate that it must lie close to the average British date of 21 August given by Longfield (1949). From Table 1 we can derive 10 June as an average date for the beginning of the flying season, thus obtaining an estimate of 72 days for its total duration. If we assume that the relationship between life-span and flying season is of an order comparable to that found for *Pyrrhosoma nymphula*, substitution in the above ratio gives a maximum post-maturation life-span of 45 days. A rough check for this value can be obtained by comparing the

Fig. 21. Dorsal view of head of female adult, after copulation has occurred. The two marks left by the dorsal surface of the male inferior appendage are shown as circles on either side of the mid-line.

average date of last emergence (8 July) with the end of the flying season. This method gives an estimate of 44 days, a figure including the maturation period which, however, we may suppose to be shorter late in the season. Furthermore since adults derived from the end of the emergence period will be very scarce towards the end of their life-span, the estimated last date for the flying season may be expected to be earlier than the real one, perhaps to an extent comparable with the duration of the maturation period at that time of year. If this is so, we may reasonably expect the post-maturation maximum life-span of *Anax imperator* to be about 45 days. The maximum life-span of those adults which survive the maturation period will therefore be about 60 days. By analogy with *Pyrrhosoma nymphula* the expectation of life (at emergence) of those adults destined to survive the maturation period would be about 28 days.

The finding that in some years a greater proportion of females may emerge in the latter part of the emergence period (p. 41) may indicate that amongst mature adults females have a lower survival rate than males. In 1951 sixty-eight mature males of *Anax imperator* were marked and released during the flying season. Of these seven were subsequently recaptured, the greatest intervals between release

and recapture being 2, 3, 3, 4, 7, 16 and 26 days, respectively. One of these dragonflies was either seen again or recaptured at the pond on four separate occasions; these occurred 7, 14, 22 and 26 days, respectively, after its first release. The individual mentioned bore a conspicuous mark enabling it to be identified in flight. It is noteworthy that on more than half of the intervening days, when this dragonfly was not seen at the pond, the weather was unfavourable for adult flight. Moore (1953) has shown that weather conditions play an important part in determining whether or not adult Anisoptera will move from their roosting places to the water. It may be that mature adults are sexually capable of visiting the aquatic habitat on every fine day during the flight period. Adult density and the associated competition for beats are probably other factors influencing the frequency with which a given adult will visit the water. Thus in 1951 and 1952 the intervals separating successive captures of male individuals of *Pyrrhosoma nymphula* were long early in the flying season when the density was high, but short later on when the population was small (Corbet, unpublished observations). Again, in 1951, it was found that new arrivals tended to replace previous residents at the pond (Corbet 1952). It is possible, therefore, that intensity of sexual drive is a factor determining whether or not an individual can establish a beat, and that adults which have copulated recently are obliged to yield to new arrivals. At present it may be said that during the reproductive period the frequency with which male adults visit the aquatic habitat is dependent both on the weather and on the prevailing density of other dragonflies.

It appears that late in life the colour of the female abdomen may turn from green to blue. From Table 17, which summarizes the first occasions upon which blue females were seen in 1951-53, it appears that in a normal year this colour change may take place after about 2 weeks of mature adult life. Since this period probably represents the normal expectation of life of those adults surviving the maturation period, it is clear that blue females will not be encountered frequently. Blue females were seen most often in 1952 but not at all in 1953. This suggests that the colour change may be brought about directly or indirectly by prolonged exposure to high temperatures.

(*d*) *Flight rhythm*

Moore (1953) observed that maximum density of mature male dragonflies over water occurs at about 1300 B.S.T. Although no quantitative records were obtained, an impression was gained that a similar pattern of activity existed at the Fish Pond. The number of adults over water seemed to show a regular decrease (depending upon the weather) after about 1600. Nevertheless they were seen frequently at the pond later in the day; for example, on 19 July 1951 a female was observed ovipositing at 1956 h.

There were indications that the pattern of normal flight described above was interrupted shortly before dusk by a phase of crepuscular activity. This phenomenon was observed on many nights, although detailed records were kept on only three. From 1900 to 2000 there would be very few, perhaps no, dragonflies over

the pond; then between 2030 and 2100 adults of both sexes would arrive quite suddenly from the surrounding common. They would establish beats promptly, and then feed vigorously for periods of about 20 min. Five individuals, four females and one male, observed on 8 July 1951 remained at the pond for 17, 21, 21, 22 and 23 min respectively. At the end of this time they would leave as abruptly as they had come. Clashes were seen occasionally between individuals whose feeding beats lay in juxtaposition, and such encounters sometimes led to the expulsion of one of the participants, but in general clashes were far less frequent than they would have been under conditions of a similar density in daytime. During their crepuscular flight, adults seemed fully occupied with the process of feeding. An indication of the possible temporal pattern of this phase is shown in Fig. 22. In mid-July 1951 this flight ceased at about 2130, the latest individual being seen to leave at 2136 (18 July). *Aeshna grandis* (L.) was also seen flying at

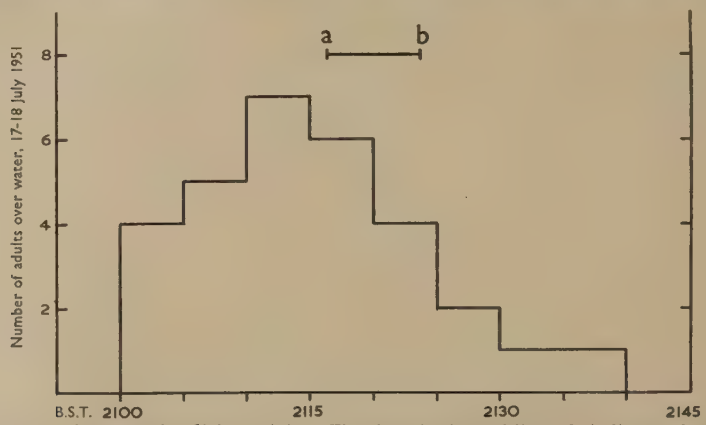

Fig. 22. Pattern of crepuscular flight activity. The short horizontal line, *ab*, indicates the duration of a short feeding visit made by a young male of *Aeshna grandis* (L.) on 16 July 1951.

dusk; on 16 July 1951 an individual fed at the pond for 8 min, from 2116 to 2124. Moore (personal communication) reports having observed seven adults of this species feeding over a ditch at Oulton Broad, Suffolk, at 2100 B.S.T. on 28 July 1947. It is clear that more data are needed to establish the status of this crepuscular phase of activity. Although particularly careful watch was kept, nothing was seen resembling the crepuscular 'dance' reported for *Anax junius* (Drury) by Rau (1945). Adults were often observed feeding over the common shortly before dusk, but they were invariably flying singly and not in association with others. It is possible that the dance seen by Rau was a modification of the crepuscular feeding flight resulting from the exploitation of a localized swarm of some food organism. Thus it may not have represented an expression of truly gregarious behaviour. It is relevant to mention here that the writer has observed a well-defined dusk feeding flight in *A. imperator* on the shores of Lakes Victoria (Uganda) and Tanganyika (Tanganyika).

At the Fish Pond, only a few adults were seen to alight at the conclusion of the

dusk flight; low light intensity made it difficult to follow them by eye. Those watched alighted singly. On no occasion were nocturnal aggregations encountered, as reported for *A. junius* and other Anisoptera by Bick (1949) and Penn (1950), although careful searches were made on many occasions. Towards the end of the daily flight period, adults repeatedly settled and took off again. Usually the spot where they finally alighted faced the setting sun, and at the Fish Pond was either amongst heather or about 2-3 m above the ground on a birch tree. A female disturbed during 'sleep' (see Rau & Rau 1916) flexed its abdomen dorsally, perhaps as a defence posture, but was unable to fly until it had vibrated the wings for about 5 min. Moore (1953) found it likely that both *Sympetrum striolatum* (Charp.) and *Aeshna cyanea* (Müller) require an initial period of wing vibration before flight if their body temperature is low, a view in accord with the findings of Sotavolta (1954). In *Anax imperator* the wings are not closed dorsally during sleep.

(*e*) *Food*

Although little concise information exists concerning the food of adult *A. imperator*, it appears to consist largely of small Diptera. Indeed, the enlistment of *A. junius* as an agent in the biological control of malaria on account of this food preference was at one time seriously considered (Lamborn 1890). It is doubtful, however, whether adults discriminate regularly between prey species. On several occasions both at the Fish Pond and at Madingley, Cambridgeshire, adults of *A. imperator* have been seen to capture other Odonata. These included *Sympetrum striolatum, Pyrrhosoma nymphula* and other species of Coenagriidae.

(*f*) *Mortality*

Dead adults are seldom found. It seems likely that considerable numbers die after having been forced into the water during clashes with males. After one such encounter on 6 July 1951 a male was seen to be unable to rise from the water. Again, on 14 June 1953 a mature female was discovered dead on the surface. On 11 July 1953 a dead male was found in the water; this individual possessed characteristic marks on the compound eyes, indicating that it had previously been grasped by another male.

There are probably very few regular enemies of mature adults. Predation has been seen only once: on 17 July 1951, during a crepuscular flight, a hawk made a successful stoop on an adult over the pond at 2115 h. The bird was thought to be a kestrel (*Falco t. tinnunculus* L.). Moore (1952*c*) remarks that the hobby (*F. s. subbuteo* L.) is probably the only British bird which habitually feeds on Anisoptera. Moore (personal communication) has observed both the house-sparrow (*Passer d. domesticus* (L.)) and the spotted flycatcher (*Muscicapa s. striata* (Pall.)) making unsuccessful attempts to catch mature adults of *Anax imperator*. Kennedy (1950) makes it clear that adult Odonata are seldom preyed upon extensively by birds. Moore (1952*c*) has suggested that most adult Odonata die of starvation due to the indirect effects of bad weather and physical damage

resulting from clashes with other dragonflies. The survivorship curve of *Pyrrhosoma nymphula* (Corbet 1952) accords with this view.

(*g*) *Discussion*

Until more is known about longevity and dispersal, the influence of the adult stage upon the life-history must remain obscure. It seems likely that in some regions the population of mature adults in a given habitat derives mainly from a few habitats maintaining a high density, and not evenly from the whole area. The resulting variation in the temporal distribution of oviposition may be expected to influence larval populations. Thus in habitats such as the Fish Pond and perhaps Withermore Common Pond (Fig. 7), where the larval population is provided by the synchronized return of residents, oviposition may occur early enough to allow occasional uni-voltinism. In habitats supplied principally by non-resident wanderers oviposition will probably occur later and be temporally dispersed. Colmans Moor gravel pit (Fig. 7) may represent a habitat of such a type. These factors may have a slight effect upon the next generation by determining the proportions emerging in the two emergence peaks, but variation in the time of oviposition will be effectively erased by the diapause in the final larval instar.

SEASONAL REGULATION

The field studies already described have shown that, although final instar larvae may be present at all times of the year, emergence is restricted to a period of about 6 weeks, between late May and early July. Larvae entering the final instar in spring proceed directly to metamorphosis, whereas those doing so after the end of May embark upon a period of delayed development and do not metamorphose until the following spring. This period of delayed development persists when environmental conditions are otherwise favourable for metamorphosis. It can therefore be regarded as a diapause stage. Furthermore the fact that diapause is associated with larvae that enter the final instar after the end of May but not with those that do so before, indicates that diapause is facultatively determined and not inherited as an obligate feature of the life-history. It has been shown that the incidence of the diapause is controlled by a critical response to changing length of day (see Corbet 1956*a*).

The animals which have been found to exhibit facultative diapause are almost without exception bi-voltine or multi-voltine. In manifesting facultative diapause *Anax imperator* presents a special case, at least in southern England, where it is usually semi-voltine and occasionally uni-voltine. Dates given for the flying season in Germany (Münchberg 1932) and Switzerland (Portmann 1921) indicate that in these countries this species rarely, if ever, completes more than one generation in a year. Its larval ecology is probably similar both in England and in mid-Europe. In England variation in larval size is such that the winter may be passed in any instar from the 8th to the last (about the 15th). This means that less than half of a population spends the winter in diapause; for the majority it is

a period of dormancy. Thus unlike that of most uni-voltine species a population resuming growth in spring consists partly of larvae which have completed diapause and partly of those which have not. But both groups may proceed to metamorphosis, the second only if it achieves the final instar before the end of May. A consequence of this diapause mechanism will be that, whether a given population is semi- or uni-voltine, its emergence period will have the same seasonal limits; only the proportion of adults emerging in the first and second peaks will vary. It is probable, for instance, that in the southern part of its range *A. imperator* spends the winter chiefly in the penultimate instar and emerges the following spring in the second emergence peak. This would give it a slightly longer flying season than in the northern part of its range where more than 90% of a population may emerge in the first peak. The location of a diapause stage in the final larval instar can be seen as an efficient mechanism achieving synchronization of adult emergence. The fact that it is developed facultatively obviates the necessity for larvae in the penultimate instar in spring to spend a further year in the larval stage. This is done at the expense of prolonging the emergence period by about 20 days.

The ecological significance of such rigorous seasonal regulation in *A. imperator* is not clear, especially when it is recalled that severe temporal restriction of emergence results in a high mortality (Table 16). Its importance may be associated more with the high thermal coefficient for larval growth than with adult longevity. In *Pyrrhosoma nymphula*, another spring species, synchronization of the reproductive stage is clearly desirable when the average expectation of life of a sexually mature adult is only about 7 days (Corbet 1952). In *Anax imperator* it has been estimated that this value is at least 14 days, although perhaps in this species the greater powers of dispersal reduce the effective length of the reproductive period over water. The high lower temperature threshold for larval growth may set a premium upon the ability of eggs to hatch early in the summer, for it has been demonstrated that larval growth can be extremely rapid in July and August. There can be little doubt that large larvae have fewer effective enemies than smaller ones, and that the individuals achieving a large size before the period of winter dormancy will thereby increase their chances of survival. Furthermore it is possible that the non-diapause eggs may be unable to survive winter temperatures, a circumstance which would itself impose a late limit on the flying season.

In northern populations, the chief importance of the diapause may be concerned with restricting the flying season *per se*, as an adaptation to avoid competition with the 'high-summer' aeshnids which colonize similar habitats in temperate regions. In this connection it is noteworthy that *A. imperator* is typically a mediterranean species and under normal conditions does not experience competition with other aeshnids occupying similar ecological niches. The ability to restrict its emergence to spring and early summer may thus permit it to exist in northern habitats from which it would otherwise be excluded. *A. imperator mauricianus* (Hagen), which is assigned to this species, has a tropical distribution and exhibits no diapause, although experiencing a regime of almost unchanging photoperiods.

It may be that a physiological cline exists between the two subspecies of *A. imperator*; to discover the lowest latitude in which diapause is a regular feature of the life-history might throw an interesting light on the evolution of seasonal regulation.

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SUMMARY

NOTE. The times in the summary are given as British Summer Time. One hour should be substracted in order to obtain Greenwich Mean Time.

1. The life-history of the emperor dragonfly, *Anax imperator* Leach, has been studied under natural conditions with the object of determining the principal ecological factors concerned in its seasonal regulation. Particular attention was paid to a population existing at high density in a pond near Reading, Berkshire.

2. The eggs are laid in surface water-plants, and develop in the region of highest temperature and light intensity. They hatch in about 3 weeks. Oviposition lasts for about 8 weeks each year, usually extending from early June to early August. The protracted period of oviposition and the direct development of the eggs combine to endow the hatching larval population with a wide temporal variation.

3. Estimates of growth-rate were affected by three factors: non-random spatial distribution of larvae with respect to size; size-overlapping between age-groups; and errors arising from the use of successive sample means for computing growth in insect populations.

4. Duration of the larval stage is usually about 2 years, but exceptionally it may be completed in 1 year. Larval growth is restricted to about 6 months each

year, from May to October. A few precocious larvae hatching from eggs laid early achieve the penultimate or final instars by the first autumn, and emerge as adults the following spring. The remainder, usually composing more than 90% of an emergence-group, attains an average length of about 24 mm (range 7-42 mm) before growth ceases in autumn. Growth is resumed in May, and the final larval instar is entered in August, approximately 12 months after hatching. The next 9 months are spent in the final instar without visible growth, and emergence takes place the following spring between mid-May and mid-July, about 23 months after hatching.

5. The thermal coefficient for growth is relatively high, but two factors extend the duration of the larval stage: a high 'lower temperature threshold' for growth, and a diapause in the final instar. The diapause is facultative and only affects larvae entering the final instar after May.

6. During the first summer the largest larvae of the age-group are found amongst the *Littorella* and the smallest amongst the *Potamogeton*. This size-gradient persists until the following spring, but has disappeared by July. From August onwards, final instar larvae congregate in the *Hypericum* mats; here they remain until metamorphosis begins in April.

7. Small larvae have a striking colour pattern of black and white transverse bands which persists only during the first year of larval life. This colour pattern may serve to protect young larvae from predation by the senior age-group.

8. An earlier study of larval duration in *Anax imperator* is re-examined, and a different interpretation placed upon the results.

9. Sample data from other larval habitats are discussed. In England *A. imperator* is chiefly a 'spring' species, but possession of a facultative diapause allows a small proportion to exist as a 'summer' species, and thereby obviates the necessity for full-grown larvae to prolong the life-history by one year.

10. Metamorphosis is observed in nature only from early April to early July. Its progress has been studied by taking regular samples and assigning larvae to one of six arbitrary stages. The first external signs of metamorphosis are visible 45 days before emergence.

11. Metamorphosing larvae fall into two groups, the main population showing early and well-synchronized metamorphosis, and a small fraction which metamorphoses late and is temporally dispersed.

12. Non-random movements during metamorphosis have been studied by selective sampling in different plant zones and by analysing recaptures of marked larvae. These movements relate to the stage of metamorphosis that has been reached, and affect the representative properties of samples taken at this time.

13. Metamorphosis usually begins in mid-April. Larvae then leave the *Hypericum*, in which they spent the previous winter, and move to the *Littorella* during stage 2. Stage 3 is spent in the *Hypericum* and stage 4 in the *Potamogeton*. Two days before emergence, when in stage 6, larvae move by night to the supports where they remain until emergence. Larvae may suffer a mortality of 54% during metamorphosis.

14. Emergence of *Anax imperator* has been studied quantitatively for three successive years by making collections of exuviae daily during the emergence period. Factors influencing the practicability of this technique are: restriction of available emergence supports, diurnal rhythm of emergence, permanence and size of exuviae, and physical features of the habitat.

15. Yearly emergence is restricted to a period of 40-50 days, usually extending from late May to early July. First dates of emergence vary from mid-May to early June but last dates vary only from 5-12 July.

16. The time-frequency curve of emergence is asymmetrical with an early peak. Emergence is well-synchronized in consequence of the retarding effects of diapause the previous summer, and about 90% of an annual population of adults emerge during the first 10 days of the emergence period.

17. The emergence curve is bimodal. The first peak is well-synchronized and includes 90-95% of the yearly population; it represents the emergence of larvae two seasons old which entered diapause the previous summer and have spent 9 months in the final instar. The second peak, widely dispersed temporally, contains 5-10% of the yearly population; it occurs about 25 days after the first peak, and represents the emergence of larvae, probably one season old, which have overwintered in the penultimate instar, entered the final instar in spring, not undergone diapause, and spent only 40 days in the final instar.

18. The sex ratio of emerging adults is usually about 0·96 (49% males). In the first emergence peak there is no indication that either sex emerges earlier, but in the second (when it is well-developed) there may be a preponderance of females. Thus over the whole emergence period males tend to emerge earlier than females. Females may so predominate in the second peak as to reduce the sex ratio of the whole emergence-group to about 0·89 (47% males).

19. Most larvae moved to the southern end of the Fish Pond in order to emerge, preferring shaded regions.

20. Usually, a day-group of emerging larvae leaves the water shortly after dusk, about 2145 h. Larvae remain motionless on the emergence supports for about 45 min; eclosion follows and the adults are fully formed soon after 2400 h. The maiden flight is closely synchronized and occurs at about 0430 h.

21. When evening emergence is prevented by low air temperatures occurring after the method of respiration has changed from rectal to spiracular, divided emergence occurs, part of a day-group postponing it until early the next morning.

22. Mortality during emergence has been studied quantitatively. Deaths due to incomplete ecdysis and incomplete expansion of the wings were density-dependent and totalled from 5 to 10% of an annual emergence-group. Predation by blackbirds accounted for from 3 to 5% of the annual population and appeared to be independent of density. Low air temperatures and strong winds during emergence resulted in increased mortality. Usually about 90% of an emergence-group survive emergence.

23. Newly emerged adults fly shortly before sunrise. For the maiden flight they fly away from water and may fly several hundred metres before alighting.

This orientation is perhaps an adaptation directed towards protecting teneral adults from the aggression of sexually mature males.

24. Adults fly again during the first day, and remain away from water for the next 2 weeks. During this maturation period they fly often, feed, shun water and show no sexual response to other dragonflies.

25. After a minimum of 9 days of adult life, the first males begin to exhibit sexual behaviour over water; females return to water to oviposit from 2 to 3 days later. Copulation occurs promptly upon arrival of a female, and is followed almost immediately by oviposition. Both sexes probably return to the water frequently after the first mating. Males are capable of copulating more than once.

26. The expectation of life at emergence of those adults destined to survive the maturation period is probably about 4 weeks, and the maximum life-span approximately $8\frac{1}{2}$ weeks.

27. The greatest flight activity of mature males occurs at about 1300 h, but there are indications of a crepuscular phase over water occurring between 2030 and 2100 h. Feeding, but very little sexual activity, has been observed at this time.

28. Considerable adult mortality results from damage sustained in sexual clashes with other dragonflies over water. Predators of mature adults are few.

29. *A. imperator* is a spring species, diapause in the final larval instar resulting in a closely synchronized emergence. Ecological advantages of such rigorous seasonal regulation may be: to synchronize the appearance of the short-lived reproductive stage; to avoid adult competition with other species of Aeshnidae; to ensure that the non-diapause eggs hatch before the winter; and to enable larval growth to proceed rapidly in summer, when water temperatures are highest. A disadvantage of synchronized emergence is that it results in increased mortality during emergence.

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DIFFERENCES IN THE FLOWERS VISITED BY FOUR SPECIES OF BUMBLE-BEES AND THEIR CAUSES

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(With 4 Figures in the Text)

INTRODUCTION

The feeding plants visited by different species of *Bombus* have been recorded in many countries and most observers are agreed that bees of each species tend to frequent different flowers but that there is considerable overlap nevertheless. The literature on this subject has been reviewed recently (Brian 1954) and will not be discussed again in detail.

The object of this study was to determine what differences existed in one small area in the feeding plants of the four common species of *Bombus* present, and the cause of these differences. Many observers have commented on the connection between the length of the corolla tube of the flower and the tongue length of the bumble-bees that visit it but other factors also seem to influence the choice of flower by the bee. In many cases under natural conditions two or more of these factors may be confounded, for example corolla length and flower colour. In this paper an attempt has been made to determine the importance to bumble-bees of a number of these factors independently.

METHODS

(*a*) *Counts of bees in the field*

The pollens collected by *B. lucorum* L., *B. agrorum* Fabricius and *B. hortorum* L. have been determined by identification of the pollen residues in larval meconia (Brian 1951). This provides an objective method of sampling the entire pollen collection of a colony. Unfortunately it is not possible to sample nectar collection in the same way so that the usual method of counting the number of bees seen foraging on different plants has been used. As a means of assessing the importance of different nectar plants to any one species of bee this method is not very reliable since the results depend entirely on the observer's movements. But for the purpose of comparing the relative importance of any one plant to the different bee species it is more reliable, provided that counts are not all made on the same groups of plants or in the same year, thus ensuring that many different individual bees are involved.

The area studied was on the north bank of the Firth of Clyde, and its flora has already been described (Brian 1951). Counts were made frequently throughout the summers of 1950, 1952 and 1953. A few plants that grew in quantity at some distance from the centre of the area (e.g. *Calluna*, *Rhododendron*) were only visited once or twice but most of the totals are made up from many small daily counts.

Queens and workers of each species were counted separately; males were not counted at all. *Bombus terrestris* L. workers have been included in the *lucorum* worker totals since the two species are not readily distinguishable in the field and, judging by the number of queens in spring *lucorum* was much the most abundant species. All the *agrorum* seen in the area belonged to the subspecies *septentrionalis* Vogt.* In general the counts on any one flower were reasonably consistent from year to year and though at the time they were recorded separately for each half month, the sum for all three years is given in all tables in this paper. In 1952 and 1953, wherever plants visited by bumble-bees were found growing in two habitats, counts were made separately in order to assess the importance of environment to the bees independent of flower form, colour, etc.

(*b*) *Experiments with paper flowers*

In addition to these natural experiments artificial flowers were used. These were set out in a garden and visited by free flying bees. The 'flowers' were simple funnels of coloured paper, waterproofed at the base to hold a drop of syrup and held on wire 'stalks' about 6 in. above the ground: variations in the shape, colour, etc., of the 'flowers' are described under the individual experiments. The reactions of bumble-bees to artificial nectar sources do not seem to have been described before in any detail; indeed very few cases of bumble-bees visiting artificial nectar sources have been described (see Brian 1954). In general bumble-bees were not found to be such good subjects for experiments of this sort as honey-bees. In the first place bumble-bees almost certainly do not communicate to nestmates the position of a source of food. This limits the number of visitors but in practice was not found a serious drawback, chiefly because once one or two bumble-bees had been introduced to the feeding place (by holding them over a 'flower' in a darkened tube until they began to drink) and were visiting the 'flowers' regularly others would come of their own accord, provided the experiment was carried on for some days. It is probably significant that these results were obtained in a flower garden which was something of an oasis in May and June surrounded by a desert of flowerless arable fields and moorland. It seems reasonable to suggest that newcomers were attracted to the 'flowers' by the perception of other feeding bees; at any rate, as will be described later, regular visitors to the feeding place were not indifferent to the presence of other bees. A serious difficulty in the use of artificial flowers for comparisons between species was that *hortorum* workers could not be persuaded to visit them. A certain number of bees of all species refused to settle down and drink when held over a 'flower' but not a single *hortorum* would do so.

* Professor O. W. Richards very kindly identified some individuals.

In addition no *hortorum* visited the 'flowers' once a good band of visitors had been obtained, even though they were working flowers nearby. Incidentally, although many queens were introduced to the flowers and although they drank and orientated none ever returned except for a single *B. lapidarius* L. (the only *B. lapidarius* seen in that area in seven years) who found the flowers for herself and paid repeated visits. This was unfortunate as feeding queens in such a way would be an easy method of encouraging nests at a vulnerable stage and would also probably make it easy to discover them early in the season.

Another difficulty was that the bees visited the 'flowers' spasmodically. Thus in inclement weather, not sufficiently bad to prevent foraging, bees came readily; for example, throughout an hour of light rain one *agrorum* paid eleven visits, averaging 2 min on the flowers and 3·3 min away, but as soon as the sun came out this regular behaviour ended. A bee would pay brief visits to the 'flowers' and then go off on to real flowers in the vicinity paying another visit perhaps later in the same trip with pollen on its legs. Increasing the concentration of the syrup held the bees to the artificial flowers a little longer but not indefinitely: evidentially the urge to collect pollen was too strong. Often regular marked visitors would cease to come to the 'flowers', at any rate during observation periods, for a few days and then return again.

All the experiments with artificial flowers, to be described later, were designed to explore differences in species preference and the bees were offered a choice of 'flowers'. Unfortunately visitors were influenced in their choice not only by the type of flower but by the presence of other bees already there. Furthermore, bees of any one species sometimes showed individual differences in their preferences. These sources of error introduced by individuality and by the influence of other bees would be expected to affect the behaviour of bees 'foraging' in captivity but Kugler (1943) does not appear to have taken account of them.

COROLLA TUBE LENGTH AND TONGUE LENGTH

(*a*) *Measurements*

Since some flowers vary in size in different localities it was desirable to measure the flowers actually visited by the bees in the area studied. These measurements are given in Table 1, each figure being the average of ten flowers from different plants. In some flowers it is easy to decide exactly what length of tongue would be required to reach the base of the corolla tube but in flowers which converge gradually to the base or which can be opened it is not so easy to say how far in the bee might be able to push its head. A subjective factor enters here but where the figures can be compared with those given by Knuth (1906-09) there is good agreement.

The tongue length measurements may be obtained from Fig. 1. Since it is possible that a cline in tongue length exists within each species it was desirable to measure the bees of the locality instead of using existing measurements. It was

found that these Scottish bees had tongues of the same length as Finnish bees (Hulkonnen 1928) and in all cases except *lucorum* were longer than Danish bees (Stapel 1933). Heavy collecting, particularly of queens, did not seem desirable and so as far as possible the tongue length of living bees was measured by persuading them to drink syrup out of capillary tubing graduated in millimetres. This method worked well with *lucorum* and *B. pratorum* L.; the bees drank readily and obviously extended their tongues to the fullest extent. Some *agrorum* behaved in the same way but others would only drink after a very long time and very few *hortorum* would drink at all. These differences in behaviour are the same as those

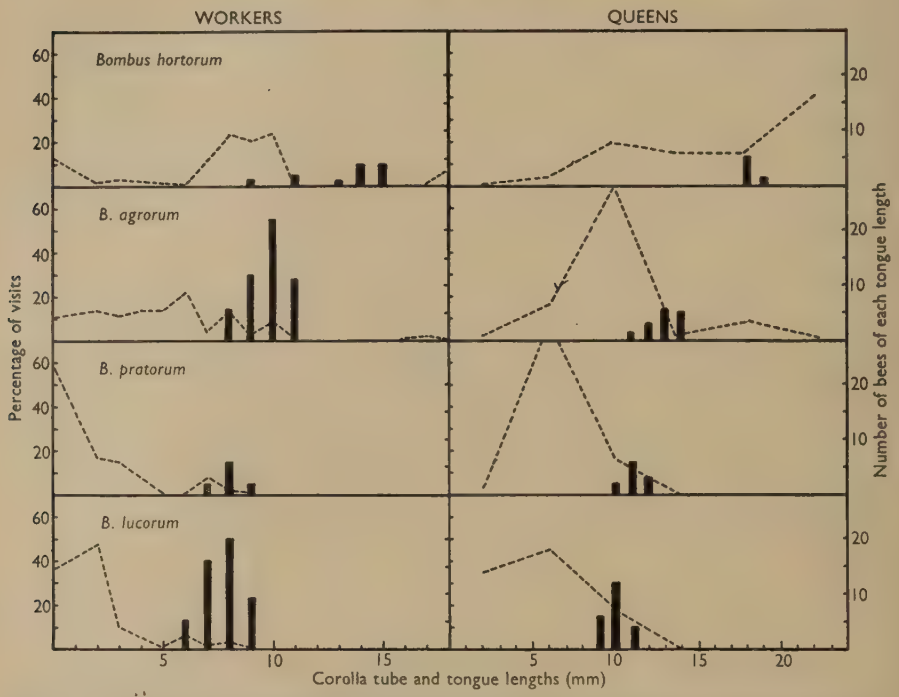

Fig. 1. The percentage of visits paid by workers and queens to flowers of different corolla tube lengths. Tongue lengths are shown as histograms.

noted when introducing bees of the different species to syrup at artificial flowers and appeared to result from differences in 'temperament' rather than from any difficulty *hortorum* might have in extending its long tongue to drink. Whereas *hortorum* was clearly dominated by the urge to escape from captivity, *lucorum* once it had found the syrup was eager for that alone until its crop was full. As a result of this difficulty all *hortorum* were killed before their tongues were measured. Some *lucorum* were measured alive and again dead and the results found comparable to the nearest millimetre so that the two methods of measurement have not been distinguished in Fig. 1.

(b) Results

The number of bees counted on different nectar producing flowers are given in Table 1 which shows, as Hulkkonen (1928) and others have already demonstrated

Table 1. *Number of 'legal' nectar visits paid to flowers with corolla tubes of different lengths*

A dash indicates that no visits were recorded because the plant was not in flower when bees of that species and caste were flying; 0 indicates that no visits were recorded although flower and bee were seen at the same time.

	Length of Corolla Tube in mm	Queens				Workers			
		luc.	*prat.*	*ag.*	*hort.*	*luc.*	*prat.*	*ag.*	*hort.*
Rubus idaeus Linn.	open	–	–	3	0	41	123	15	0
Geranium sp.		–	–	2	0	0	17	3	0
Blackberry		–	–	–	–	128	72	22	21
Acer pseudo-platanus L.		50	2	0	–	–	–	–	–
Tilia		–	–	–	–	10	5	0	0
Trifolium repens L.	2	–	–	2	1	218	38	44	2
Cotoneaster spp.		–	–	0	0	2	14	0	0
Veronica garden var.		–	–	–	–	13	17	13	0
Centaurea nigra L.	3	–	–	6	0	1	14	8	0
Calluna vulgaris Hull		–	–	–	–	36	0	6	0
Cirsium palustre Scop.		6	–	–	–	13	43	30	6
Ribes sanguineum L.	4	11	17	2	0	–	–	–	–
R. nigrum L.		46	18	14	1	–	–	–	–
Knautia arvensis Coult.	5	–	–	–	–	1	–	25	1
Lathyrus pratensis L.		–	–	–	–	0	–	30	0
Lotus uliginosus Schkuhr.	6	–	–	–	–	30	–	42	0
Melampyrum pratense L.		–	–	–	–	0	–	47	0
Brassica garden vars.	7	6	3	35	4	0	18	8	8
Lavandula spica Cavanilles		–	–	0	0	0	12	9	10
Glechoma hederacea L.		3	2	36	4	–	–	–	–
Linaria Mill.	8	–	–	1	0	0	3	24	17
Fuchsia garden var.		–	–	–	–	0	–	18	5
Prunella vulgaris L.		–	–	–	–	7	1	12	18
Aubretia deltoides DC.	9	22	3	63	18	–	–	–	–
Stachys sylvatica L.		–	–	2	0	0	–	8	34
Vicia sepium L.	10	0	0	198	9	0	0	12	20
Trifolium pratense L.		–	–	–	–	0	–	25	20
Ajuga reptans L.		0	0	20	3	–	–	–	–
Cheiranthus cheiri L.	11	4	5	94	4	–	–	–	–
Endymion nonscriptus Garcke, E.B.		1	0	14	3	–	–	–	–
Melandrium rubrum Garcke, E.B.	13	0	0	3	8	–	–	–	–
Primula garden vars.	15	0	0	2	19	–	–	–	–
Symphytum officinale L.	17	0	0	39	15	0	0	1	0
Vicia faba L.	19	0	0	3	16	–	–	–	–
Lonicera periclymenum L.	21	–	–	0	7	0	0	0	7
Aquilegia garden var.	22	0	0	2	70	0	0	0	4
		143	50	541	182	500	377	402	173
Total number of visits				916				1452	

Table 2. *Values of* χ^2 *for comparisons of the number of visits paid to different corolla lengths by different species and castes of* Bombus

All values of χ^2 are $P<0{\cdot}1\%$.
In some cases corolla lengths have had to be grouped to obtain sufficient numbers to test and the degrees of freedom for each test are given in brackets.

		lucorum		*pratorum*		*agrorum*		*hortorum*	
		queens	workers	queens	workers	queens	workers	queens	workers
lucorum	queens		38·2 (2)	19·2 (2)		*		*	
	workers				77·1 (3)				
pratorum	queens				52·7 (2)	202·5 (3)		*	
	workers						315·8 (5)		
agrorum	queens						235·8 (3)	325·3 (5)	
	workers								182·8 (6)
hortorum	queens								189·4 (3)
	workers								

* These pairs of species have not been compared since the difference must inevitably be highly significant.

in other countries a definite connection between the tongue length of the bee and the corolla length of the flowers visited. To test the significance of these results by the χ^2 test all flowers of the same corolla length have been grouped together and the frequency of visits by the different species and caste of bees compared; the results given in Table 2 show that all the differences between species, both queens and workers, are highly significant.

The difference between queens and workers of the same species are also all highly significant (Table 2) which is perhaps to be expected, since the queens in

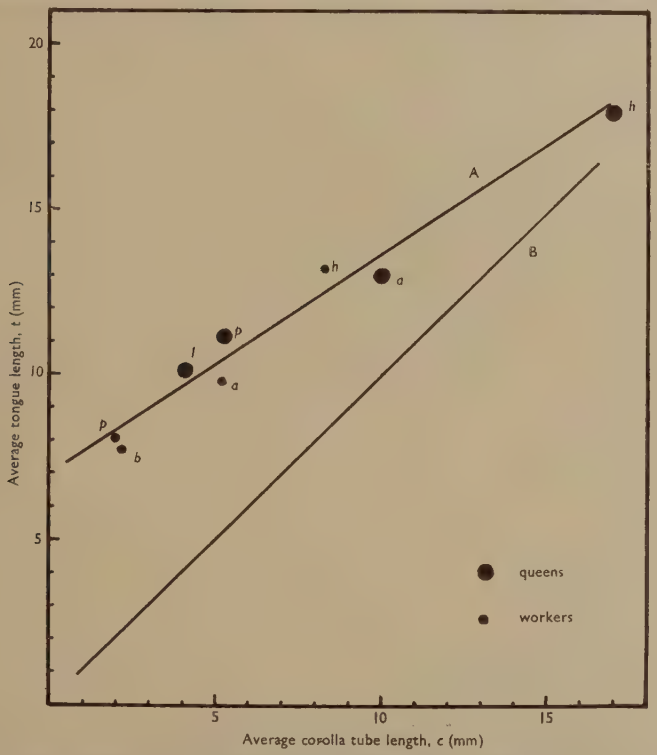

Fig. 2. The relation between average tongue length and average corolla tube length of flowers visited by queens and workers of *Bombus lucorum* (*l*), *B. pratorum* (*p*), *B. agrorum* (*a*), and *B. hortorum* (*h*). A, regression line $t = 0{\cdot}679\ c + 6{\cdot}81$. B, theoretical line (see text).

each case have slightly longer tongues than their workers. But since the overwintering queens (whose flower visits form the bulk of the queen records) emerge from hibernation a month or more before the first workers are hatched, queen and worker do not choose their flowers from the same flora (see sub-heading to Table 1).

Fig. 1 shows the percentage of visits paid by bees of each species to flowers of different corolla lengths (these have been grouped in the case of the queens) together with the tongue lengths of the bees. From this it can be seen that all species of bees visit flowers with a corolla tube considerably shorter than their

tongue. They evidently 'prefer' not to have to extend this fully nor to push their head right into the flower. Undoubtedly this behaviour will make for increased speed of working and will still lead to a division of the flora provided that bees of all species behave in the same way. That this is indeed the case for bumble-bees has been shown (Fig. 2) by plotting the average tongue length of each caste and species (from the data in Fig. 1) against average corolla tube length of flowers visited (calculated from all visits recorded in Table 1). The regression is significant (P, 1-2%) but the slope of the regression line, A, does not differ significantly (P, 10-20%) from the theoretical line, B, where the relation between tongue length and corolla length of flowers visited is the same for all lengths.

One consequence of this discrepancy between tongue length and average corolla tube length is that field data cannot be used to determine whether the correlation between tongue and corolla tube length results from innate or learned behaviour. Lie-Pettersen (1906) for example argues that because *lucorum* does not normally visit *Digitalis purpurea* although its tongue is long enough to reach the nectar, it

Table 3. *Number of 'illegal' nectar visits paid to nectar producing flowers with corolla tubes of different lengths*

	Length of corolla tube in mm	Queens		Workers		
		luc.	*prat.*	*luc.*	*prat.*	*ag.*
Geranium garden var.	open	–	–	4	–	–
Lathyrus pratensis L.	5	–	–	63	–	–
Lotus uliginosus Schkuhr	6	–	–	43	–	16
Erica tetralix L. and *E. cinerea* L.	7	–	–	76	–	–
Digitalis purpurea L.	7	–	–	–	2	1
Vicia sepium L.	10	–	–	20	28	–
Dicentra spectabilis L.	12	4	1	8	–	–
Melandrium rubrum Garcke E.B.	13	–	–	7	–	–
Symphytum officinale L.	17	28	17	5	10	–
Aquilegia garden vars.	22-40	2	–	37	–	–
Total number of visits		34	18	263	40	17

must lack the instinct to visit this flower. But since it has been shown that *lucorum* workers pay few visits to any flowers of this corolla tube length (7 mm) the argument is untenable. Kugler's (1943) contention that each bee must learn the flowers best suited to its tongue length seems more reasonable.

COROLLA BITING

(*a*) *Difference between species*

The question of corolla-biting is closely bound up with the corolla/tongue length relationship and has been much discussed. There is no doubt that the short-tongued bees form the majority of the biters and hole users; in this case *lucorum* and to a lesser extent *pratorum*. Hulkkonen (1928) gives a table showing the number of illicit visits that he recorded in Finland and Table 3 gives the corresponding results in this study.

There are two schools of thought with regard to the differences shown by the species in this respect. Lie-Petterson (1906) and Pittioni (1942) in part consider that the differences in behaviour are instinctive. As evidence Pittioni instances the fact that *Bombus mastrucatus* Gerst bites flowers which have corolla tubes short enough to be visited legitimately, e.g. *Digitalis ambigua*. The present study would add the biting of *Lathyrus pratensis*, *Lotus uliginosus* and *Erica* sp. by *lucorum* as further examples, but since it has been shown that *lucorum* normally restricts its visits to flowers with much shorter corolla tubes than these, the argument loses its force unless it can be shown that *lucorum* bites flowers with a corolla tube of 3 mm or less. Hulkkonen (1928) gives and comments on only one example of this, namely a *lucorum* biting *Althaea*; however, the narrow space between stamens and corolla in this flower make it awkward if possible for a *lucorum* to reach the nectar normally. Kugler (1943) expounds the other school of thought, that it is entirely a matter of learning; all species bite flowers whose corolla tubes are too long for them to visit normally. If this is the case the fact that *hortorum* and other long-tongued bees do not bite flowers normally pollinated by butterflies and moths must be explained, and Kugler considers that it results from the relative weakness of their extended mouthparts. He did not experiment on the matter, however.

The strength of the mandibles of the different species was tested by confining the bees individually in 3×1 in. glass tubes, darkened all round and closed at the end by a dock (*Rumex* sp.) leaf, care being taken to arrange the midrib symmetrically in all cases. Under these conditions all bees used their mandibles readily and the time taken to bite a way out was recorded for ten bees of each caste and species. The time taken depended partly on the part of the leaf first attacked and also on the size of hole made (many bees made unnecessarily large holes) but the results showed no evidence that *hortorum's* mandibles are weaker than those of *lucorum*. *Agrorum* queens and workers did appear to have more difficulty, also *pratorum* workers. The few honey-bees tested never succeeded, as would be expected, in biting a way out. The average time taken by ten *lucorum* queens was 5·0 min and ten *hortorum* queens 5·6 min. It would appear then that strength of mandibles is not the important factor in deciding whether a bee will or will not bite flowers; strength of maxillae could not be investigated in this way but the mandibles are often used by *lucorum* and, according to Werth (1949), always by *lapidarius*. Difficulty in inserting a long tongue into a small hole while standing (it is easily done when flying) may be a more potent factor as Kugler has also suggested.

Little new evidence has been brought forward for or against the instinctive hypothesis, but some of the evidence previously used on both sides has been shown to be wrong, and the matter must still be considered unproven. It does seem, however, that there are some grounds for supposing that an inherent difference in behaviour exists between the extremes, *lucorum* and *hortorum*. Thus while *hortorum* appears conservative and stereotyped, always visiting flowers by the obvious and correct entrance, *lucorum* is an opportunist obtaining nectar by a variety of methods. The difference in behaviour of a normal visitor and a thief is

very marked in a flower like the long-spurred garden *Aquilegia*, where *lucorum* lands on the base of the flower and then runs away from the normal opening along an inch or more of narrow spur to bite the tip. In addition to stealing by biting it collects sugar in the form of honeydew which *hortorum* does not (Hulkkonen 1928), and the author has observed *lucorum* workers visiting *Geranium pratense* for nectar at the back of the flower, which being open is perfectly accessible from the front. Since the majority of so-called bumble-bee flowers are adapted to visits from the long-tongued bumble-bees it seems reasonable to suppose that they could never have evolved or maintained themselves unless these species were conservative in their habits.

(*b*) *Position of the hole*

A number of writers (see Brian 1954) have commented on cases where bilateral flowers have all been bitten on the same side in any one year and suggest that this occurs because all the bees always make new holes in unbitten flowers on the same side that they first happened to find a hole. Observations on *Lotus uliginosus* have shown that this is indeed the case. In this and some other species of *Lotus* the corolla is so shaped that a small hole occurs naturally on either side just above the calyx. In *L. uliginosus* a tongue of 7 mm is required to reach the nectar normally but one of only 4 mm if the side holes are used. In this flower, therefore, the use of holes for obtaining nectar is dissociated from the act of biting and the visiting bee is invariably presented with a hole on both sides of the flower. Workers of both *lucorum* and *agrorum* visited *Lotus* freely for nectar and pollen. Forty-three *lucorum* and sixteen *agrorum* workers were watched while they visited at least ten flowers in succession and in each case individual bees always visited either the left or the right side and no bee was seen using both sides. Twenty-eight bees used the left hole and thirty-one the right, numbers compatible with an unbiased population tendency. Left- and right-'handed' bees were seen working on neighbouring flowers so this behaviour was not caused by any differences in the size of holes on different plants and must have arisen from the methodical behaviour of the bees. In many cases stealing nectar was combined with normal pollen collection and bees behaving in this way worked faster, i.e. visited more flowers per minute, than bees collecting either pollen or nectar legitimately. As would be expected a higher proportion of *lucorum* workers were stealing than of *agrorum*.

ABSENCE OF NECTAR AND THE BEHAVIOUR OF BEES ON FLOWERS YIELDING POLLEN ONLY

Hulkkonen (1928) has shown that *lucorum* is more common on flowers which yield pollen only than other species of *Bombus* in Finland and the same thing has been found in this area (Table 4). This might arise in two ways; either through differences in the attractiveness to the different species of pollen unaccompanied by nectar, or from the fact that most pollen-only flowers are of the open type

which, in nectar flowers, are visited mainly by *lucorum* as already described. In the latter case the behaviour would arise as a carry-over from nectar collecting behaviour. Both factors are probably operative and the evidence for each will be considered separately.

(*a*) *The attractiveness of pollen with or without nectar to different species*

It is possible that this might be determined directly by inducing bees to come to an artificial source of pollen, but this has not been attempted. Instead the proportion of bees of different species gathering only pollen from flowers yielding nectar and pollen has been compared. *Lotus uliginosus* was the flower found most

Table 4. *Number of visits paid to flowers by bees collecting pollen without nectar*

	Length of corolla tube in mm	Queens				Workers			
		luc.	*prat.*	*ag.*	*hort.*	*luc.*	*prat.*	*ag.*	*hort.*
FLOWERS YIELDING POLLEN ONLY									
Conopodium majus Lor. and Barr.	open	–	–	–	–	30	1	–	–
Filipendula ulmaria Maxim.		–	–	–	–	119	2	–	–
Rosa spp.		2	–	–	–	75	27	1	–
Helianthemum garden vars.		1	–	–	1	27	14	–	–
Papaver orientale L.		2	–	–	–	92	1	–	–
Shirley poppy		–	–	–	–	22	–	–	–
Solanum dulcamara L.		–	–	–	–	8	9	–	–
Sarothamnus scoparius Wimmer		8	1	9	4	2	2	–	1
Lupinus polyphyllus Lindl.		2	–	40	18	165	6	8	18
FLOWERS YIELDING NECTAR AND POLLEN									
Potentilla erecta Räusch	open	–	–	–	–	14	1	–	–
Lotus uliginosus Schkuhr	6	–	–	–	–	123	–	15	–
Melampyrum pratense L.	6	–	–	–	–	2	–	–	–
Digitalis purpurea L.	7	–	–	–	–	–	–	10	2
Lonicera periclymenum L.	21	–	–	–	–	–	2	–	–
Aquilegia garden vars.	22-40	–	–	1	6	18	59	1	9
Total number of visits		15	1	50	29	697	124	35	30

suitable for this purpose and this was visited by *lucorum* and *agrorum*. Out of 159 *lucorum* visitors 123 were pollen-only collectors; out of 71 *agrorum* only 15. There was thus a highly significant ($\chi^2 = 67{\cdot}4$, $P = 0{\cdot}1\%$) difference between the species in the numbers of pollen-only collectors. It is unlikely that the difference in method of nectar collection described in the previous section, legal in *agrorum* and illegal in *lucorum*, has any bearing on the matter, since bees combining pollen and illegal nectar collection worked faster than those collecting pollen and nectar normally, and therefore presumably found it as easy to work in this way. It would seem that the difference between the species must be instinctive.

In *agrorum* it has already been shown (Brian 1952) that the larger bees collect more pollen than the smaller ones and on *Lotus* it was noticed that the larger bees

were more often pollen-only collectors than the smaller ones. The average tongue-length (taken as an indication of general size) of thirteen pollen-only collectors was 10·4 mm and that of eighteen pollen and nectar collectors 9·7 mm, but this difference is not quite significant (*t* test, $P = 5\text{-}10\%$).

Meidell's observations (1944) on *Melampyrum pratense* indicate a situation very similar to that described for *Lotus* with a higher proportion of pollen-only collectors in *lucorum* (5/19) than *agrorum* (1/10) or *hortorum* (0/5). In this area all *agrorum* seen on *Melampyrum* were collecting pollen and nectar normally; only two *lucorum*, both pollen-only collectors, were seen on this plant but their behaviour is worth recording since both were behaving in the curious way described by Meidell, placing themselves sideways over the mouth of the corolla and 'whirring' out the pollen with the wings. This has not been seen on any other plant.

(b) Type of flower visited by pollen collectors of the different bee species

Counts of the numbers of pollen-only collectors are given in Table 4. From this it can be seen that they visit the same type of flower for pollen that they visit for nectar. The majority of the flowers are of the open type and were visited by *lucorum* and *pratorum*, as were the nectar flowers of the same shape. *Agrorum* and *hortorum* on the other hand, which visit many legumes for nectar, were seen only on the two nectarless legumes, *Lupinus* and *Sarothamnus*. This would seem to support the hypothesis that bees visiting pollen-only flowers have already been conditioned to flowers of a particular shape while collecting nectar, for the length of a bee's tongue is of course of no importance when collecting pollen. Three other lines of evidence, however, suggest that there must also be instinctive differences between the species.

Firstly, *lucorum* collected pollen from *Fillipendula* and *Conopodium*, both plants with very small flowers in close inflorescences of a type not visited by bumble-bees for nectar. *Pratorum* which visit many other pollen flowers was noticeably absent from both these, which suggests that *lucorum* in its search for pollen visits flowers that differ from the normal range of flower type visited by these two species of bee.

Secondly, a difference between *lucorum* and *pratorum* was also noticed with regard to the three rather similar rosaceous flowers, *Rubus fruticosus*, *R. idaeus* and *Rosa* sp. all growing fairly close together and with flowering periods overlapping. All flowers are of the same shape, but only the two *Rubus* species secrete nectar. 169 *lucorum* were counted on *Rubus* and 75 on *Rosa*; the corresponding figures of *pratorum* were 195 and 27. The difference between bee species is highly significant ($\chi^2 = 24{\cdot}2$; $P = 0{\cdot}1\%$). This does not necessarily mean of course that *pratorum* was less common on *Rosa* because it does not produce nectar, but it is suggestive.

Thirdly, all four species collected pollen from *Lupinus* freely and their method of collecting could be watched carefully and compared. Two positions are adopted for collecting pollen. In the first the bee stands on the keel facing the standard and extends the head and mandibles forwards so that the latter touch the lower edge of

the standard. By pushing against the standard with the legs the keel is depressed and pollen forced out. Most *lucorum* and all *agrorum* and *hortorum* used this method. For small bees, however, it is impracticable, and they obtain pollen by sitting sideways across the keel and biting it open with their mouthparts. This method was used by *pratorum* (and *Apis*) and by the smaller *lucorum*. When timed this method was found slower than the first. The habit of extending the mandibles makes it rather hard to determine whether the tongue is out as well or not, but close observation showed that whereas *lucorum* and *agrorum* never extended their tongues (except in mid-air for cleaning) *hortorum* invariably did so, not apparently in a vain search for nectar (this was definitely seen with a few bees evidently unaccustomed to the flower) but as a matter of routine. The same difference was observed in bees collecting pollen from *Sarothamnus; hortorum* extended their tongues, *agrorum* did not. This suggests that *hortorum*, unlike the other species, is not psychologically adapted for the collection of pollen without nectar. They were only seen collecting pollen alone from two other plants, long-spurred *Aquilegia*, a flower which in the short-spurred form they always visit for nectar as well though the pollen and nectar collecting movements are carried out separately, and *Digitalis* which they also visit freely for nectar. In this flower the pollen collectors turn upside down, hanging from the upper side of the glove while scraping the pollen off with mandibles and legs instead of standing on the lower side and getting pollen on the back which is the normal method of approach. A number of *agrorum* workers also collected pollen in the upside-down position.

(*c*) *Conclusions*

A comparison of the species in regard to pollen collection suggests that the behaviour of *agrorum*, which nearly always collects both pollen and nectar when both are available, is primitive (as are many other characteristics of this species) and close to that of solitary bees, who for lack of a honey store in the nest must collect nectar on every trip. The behaviour of *lucorum* on the other hand, seeking pollen wherever it can be found, is specialized and reminiscent of honey-bee behaviour. It involves either carrying honey from the nest when visiting pollen-only flowers, or else visiting some nectariferous flowers on the same trip (*agrorum* does not carry honey out of the nest (Brian 1952) but the behaviour of *lucorum* in this respect is not known). It seems possible that the production of large quantities of pollen and no nectar is not always a primitive character in flowers, but may have evolved in some plants in relation to the pollen collecting behaviour of the honey-bee and bumble-bees such as *lucorum*. *Hortorum* behaves in the same way as *agrorum* in regard to pollen collection except that it always unfolds its tongue when landing on a flower whether nectar is available or not. This seems to be another, though indirect, example of the importance of the long tongue in influencing the behaviour of *hortorum*.

HABITAT

(*a*) *Exposure*

Pittioni (1938) from a wide survey classified the bees of eastern Europe according to the habitat they frequent. Of the species mentioned in this paper he found *terrestris* in dry open situations in the plains and foothills and *lucorum*, *pratorum agrorum* and *hortorum* in the damper woodlands of the plains and mountains up to 2600 m. On a small scale habitat differences have been noted between the four species studied in this area: *lucorum* visited plants in exposed positions, e.g. *Calluna* and *Erica* on the open moor and white clover in large pastures and rough grazing, while *pratorum* and *agrorum* visited plants in more sheltered positions, wood margins and scrubland. However, since the flora in exposed and sheltered situations is rather different it was necessary to determine whether the bees were being influenced directly by the habitat or by the type of flower growing there. It was noticed in the first year's count that *agrorum* was very rarely seen on white clover in pasture fields, but analysis of the pollen residues in meconia showed that 14% of pollen had been collected from that plant (Brian 1951). In subsequent

Table 5. *Number of workers foraging in exposed and sheltered habitats*

Distance from cover (yd)	*lucorum*		*pratorum*		*agrorum*	
	>20	<20	>20	<20	>20	<20
Trifolium repens	56	28	2	25	5	22
Lathyrus pratensis	33	13	–	–	8	12
Lotus uliginosus	43	103	–	–	9	26
Vicia sepium	26	7	33	0	5	42
Total	158	151	35	25	27	102

years, therefore, it was recorded whether the bees were foraging over or under 20 yd from cover of any sort (trees, hedges, bushes, etc.) for plants which grew in sufficient numbers in the two types of habitat, namely white clover, *Vicia sepium*, *Lathyrus pratensis* and *Lotus uliginosus*.

The results are shown in Table 5. The difference between *lucorum* and *agrorum* is highly significant on *Vicia sepium* ($\chi^2 = 36{\cdot}7$, $P<0{\cdot}1\%$) and white clover ($\chi^2 = 19{\cdot}8$, $P<0{\cdot}1\%$), significant on *Lathyrus pratensis* ($\chi^2 = 4{\cdot}8$, $P = 1{\cdot}5\%$) and not significant on *Lotus uliginosus* ($\chi^2 = 0{\cdot}17$). The *Vicia sepium* and white clover that were growing in the open were in short pasture grazed by cattle. The *Lotus uliginosus* and *Lathyrus pratensis* grew in rough pasture, ungrazed for the whole summer and very long and tussocky. Thus while the former fields were unsuitable for the surface nests of *agrorum* though possibly providing underground nest sites for *lucorum*, the latter provided plenty of nest sites for both species. This might account for the less striking difference in foraging habitat between *lucorum* and *agrorum* visiting *Lotus uliginosus* and *Lathyrus pratensis* if the bees forage close to

their nests or if *lucorum* forages at a greater distance from the nest than *agrorum*; alternatively the long rough grass might in itself constitute 'cover' to a foraging *agrorum*. However it is brought about though, there is a difference in foraging habitat between the two species which is independent of the type of plant growing in the two habitats.

Data on *pratorum* was only collected on two plants, white clover and *Vicia sepium* (Table 5) and is conflicting, but it is probable that, as Lie-Pettersen (1906) noted in Norway, it is a woodland bee. It was chiefly seen near cover on white clover and in the open on *Vicia sepium*, but from the latter plant it was, like *lucorum*, stealing nectar and could therefore only visit those flowers which had been bitten by *lucorum* for it does not bite holes readily itself.

(*b*) *Height above ground*

Many authors have commented or provided information on the fact that *lucorum* is a frequent visitor to forest trees in flower and in this study it was much

Table 6. *The number of bees visiting artificial flowers at different heights above the ground*

Height of 'flowers' in inches	Number of visits after feeding at 7 in. for 4 days	after feeding at 1 in. for 3 days	after feeding at all levels for 1 day
1	3	23	23
3	9	27	35
5	37	28	31
7	57	13	32
9	30	10	19
Date of experiment	June 4	June 7	June 8
No. of visits by *lucorum*	90	65	110
No. of visits by *pratorum*	46	36	30

more common on trees and shrubs, e.g. *Tilia*, *Acer*, *Crataegus*, than *agrorum* or *hortorum*. Most of the trees, however, are of the open-flowered type which from other evidence one would not expect *agrorum* or *hortorum* to visit even if they grew in the herb layer. Visits to *Crataegus* were mainly to the aphids on the leaves.

The effect of height alone was investigated on a stand of *Rhododendron ponticum* which was growing on a rock face in recently felled woodland, and was visited by three species. Many of the flowers here grew well over 20 ft from the base of the cliff, and bees were recorded as foraging either over or under 6 ft at the time they were first observed. 82 *lucorum* were counted below 6 ft and 27 above, 22 *agrorum* below and 11 above, and 27 *hortorum* below and 22 above. The difference between species in this respect is significant ($\chi^2 = 7{\cdot}5$, $P = 2{\cdot}5\%$), but *lucorum* was visiting more low growing flowers than the other two species and not vice versa as might have been expected. *Lucorum* was probably found on the lower flowers because in

many places they were more exposed, the flowers above being shaded by trees on top of the cliff. It is concluded, therefore, that height in itself is not a factor influencing the bees in their choice of flower; and indeed many individuals watched over a period of time ranged up and down freely.

This conclusion was borne out by a few experiments on artificial flowers carried out in June 1952 with *lucorum* and *pratorum*. Five paper 'flowers', provided with syrup and identical in shape and colour, were set out at the feeding place at various heights above ground. The results are given in Table 6 and show that the bees readily became conditioned to feed at a certain height, even when the difference was only a few inches, without apparently having any preference for feeding near or far from the ground.

FLOWER SHAPE

Before it was appreciated that the bees chiefly visited flowers with a corolla very much shorter than their tongue the failure of *lucorum* to visit *Digitalis purpurea*, recorded by other authors, was noteworthy. One possible explanation was

Table 7. *Number of visits paid to artificial flowers with corollas of different depths*

		Shape of flower			
		shallow	shallow inside deep outside	medium	deep
ucorum	1952	79	92	45	23
pratorum	1952	54	60	21	8
pratorum	1953	158	–	110	73
agrorum	1953	81	–	45	36
lucorum (1 bee only)	1953	10	–	17	3
Total		382		238	143

that the bees 'disliked' entering a closed flower of this type. The matter was investigated using artificial flowers made of blue paper. Six of these were set out in a circle 2-5 cm apart; all were funnel-shaped with an opening of 4·0 cm diameter but two were 1 cm deep, two 3·0 cm deep and two 5·0 cm deep. The same 'flowers' were used on four days in 1952 and eight days in 1953, being watched for about an hour on each day when all visits were recorded. The position of the 'flowers' was changed frequently and while they were being watched they were constantly replenished with syrup. In between observation periods the 'flowers' were only moved and replenished at intervals, but since this had the effect of forcing the bees on to the less popular flower shapes it does not affect the results. These are given in Table 7 and show an obvious preference for the shallow 'flowers'. There was no significant difference between the species in this respect ($\chi^2 = 4{\cdot}4$, d.f. = 4), one case of individual differences within the species was noted, however. Two *agrorum* workers paid 4, 10, 20 and 31, 14, 4 visits to shallow, medium and

deep 'flowers' respectively, this difference is highly significant ($\chi^2 = 29{\cdot}0$, $P < 0{\cdot}1\%$).

In 1952 the effect of training the bees to one type of 'flower' was noted. After feeding for one day at shallow flowers only they paid 60, 25 and 5 visits to shallow, medium and deep 'flowers'. On the following day they were fed at deep 'flowers' only and when all the 'flowers' were set out again on the day after that they paid 80, 40 and 26 visits to shallow, medium and deep 'flowers'. This indicates that the preference for shallow 'flowers' is real and not conditioned by any other foraging experience they may have had since even training to deep 'flowers' did not affect it materially (cf. contrary result described in previous section where bees were easily trained to feed at different heights).

One small experiment indicated that these results did not arise from the different inclinations at which the bees had to stand in the three types of 'flower', nearly horizontal in the shallow and nearly vertical in the deep ones. Another small experiment with deep 'flowers' made of paper of different thicknesses, transmitting different amounts of light indicated that it was not the darkness of the deep 'flowers' that the bees objected to, and in fact many natural deep flowers are very light inside. In 1952 two 'flowers' were included in each experiment which were shallow inside but deep outside and the results show that the bees judge depth from the inside rather than the outside of the flower (Table 7).

Table 8. *Visits to mixed bed of* Penstemon (*P*) *and* Digitalis (*D*)

	Number of flower visits to:					Number trips to:		
	P	P on D calyx	D	D on P calyx	D calyx	P only	D only	P & D
lucorum	88	3	0	0	10	12	0	0
agrorum	112	2	14	3	15	8	2	13
hortorum	2	0	121	8	0	0	28	2

These results at first sight conflict with those of Kugler (1943) who found depth an attractive character but are not strictly comparable since he offered a choice of concave, flat and convex surfaces whereas all these 'flowers' were concave, the deep ones being considerably deeper, relative to their width, than the ones used by Kugler. Unfortunately *hortorum* could not be included in these experiments, but since *agrorum*, which was included, also visits *Digitalis* it would appear that there is no difference between the species in regard to flower depth.

This is further substantiated by the odd fact that while *Digitalis* was visited only by *hortorum* and *agrorum* (Table 8), red garden *Pentstemons* with an almost identical (very slightly narrower 'glove') flower shape were visited only by *lucorum* and *agrorum*. Even when cut spikes of *Digitalis* were stuck in the ground among the *Pentstemon* plants the bees behaved in the same way, only *agrorum* passing freely from one flower to the other (Table 8). Some of the corollas were interchanged (they stuck well on to the calyx of the other plant) and results showed that the choice of flower was based entirely on the corolla differences, as might be

expected. Each time a *hortorum* entered a *Digitalis* corolla on a *Pentstemon* calyx it backed out hurriedly and left the plants altogether; *lucorum* were not so disturbed by the deception, they also occasionally visited the outside of the *Digitalis* flower by the calyx. *Hortorum* continued to visit the *Digitalis* after the corollas had withered, forcing themselves up the shrivelled flowers which still hung on the stem. Rather few individuals were concerned (a minimum of 7 *hortorum*, 5 *agrorum* and 3 *lucorum*) but the difference was so definite that it seems worth recording. It may be connected with the position of the nectaries, which are on the bases of the stamens in *Pentstemon* and perhaps more accessible than in *Digitalis*.

From Table 9 it can be seen that *hortorum* is undoubtedly the main visitor to flowers of the *Digitalis*-type, but it is also evident that for most of them a long tongue is required even after the bee has entered the flower. In conclusion, then, flower shape itself does not seem to be an important factor in separating the species, other things being equal all species preferring the more accessible flowers. Other aspects of flower shape, e.g. size, zygomorphy, etc., have not been investigated but comparison of the flower types visited by the different species does not show any obvious differences.

Table 9. *Number of nectar visits paid to funnel- or bell-shaped flowers*

	Length of narrow portion of corolla tube (mm)	Queens				Workers			
		luc.	*prat.*	*ag.*	*hort.*	*luc.*	*prat.*	*ag.*	*hort.*
MOUTH OF COROLLA CLOSED OR VERY NARROW									
Antirrhinum garden var.	0	–	–	2	12	1	–	4	14
Pentstemon garden var.	7*	–	–	1	–	27	1	22	–
Digitalis purpurea L.	7*	–	–	18	46	–	–	30	76
Iris spp.	13	1	1	4	8	–	–	1	9
Hosta sp.	15	–	–	–	3	–	–	–	–
MOUTH OF COROLLA WIDE									
Rhododendron ponticum L.	0	131	15	81	112	39	5	–	7
Campanula spp.	0-4	–	–	–	–	4	57	–	–
Althaea rosea Cav.		–	–	2	2	2	–	35	7
Fuchsia gracilis Lindl.	8	–	–	1	–	–	–	18	5
Calystegia sylvestris R. & S.	10-12	–	–	–	–	–	–	–	2
Tropaeolum majus		–	–	–	7	–	–	–	–
Total number of visits		132	16	109	190	73	63	110	120

* Excluding visits recorded in Table 8.

FLOWER COLOUR

The whole question of colour preferences of flower visiting insects has been much discussed and recently summarized by Kugler (1952). He points out that since there is a correlation between flower shape and flower colour the fact that long-tongued insects (bees, etc.) visit many red, blue and purple flowers and short-tongued ones (Diptera, etc.) yellow and white flowers does not necessarily indicate different inherent preferences. In this paper we are only concerned with differences between the species of *Bombus*, but Pittioni (1940) says that *terrestris* and *lucorum* have a preference for yellow and white in contrast to the other species.

Certainly in this study too *lucorum* visited more yellow and white flowers than the other three species. For example from the data given in Table 1 85% of the visits of *lucorum* workers were to yellow or white flowers and only 15% to red, purple and blue flowers. 68% of *pratorum* worker visits were to yellow and white, 40% of *agrorum* and only 23% of *hortorum* worker visits. The results from pollen sampling show the same trend (Brian 1951). On the average *lucorum* colonies collected 52% of their pollen from white and yellow flowers, *agrorum* colonies 21% and *hortorum* colonies only 12%. But the correlation between flower shape and colour is relevant here too because there are such wide differences in tongue-length between the species of *Bombus*. Of the plants listed in Table 1 nearly half (6 out of 13) of those with a corolla tube of 4 mm or less are yellow or white, but of the plants with a corolla-tube over 4 mm long less than one-third (6 out of 23) are of these colours. Furthermore when illegal visits and visits to pollen-only flowers (Tables 3 and 4) where tongue-length is not important are considered, only 58% of visits by *lucorum* workers (426 out of 740) were to yellow and white flowers, which contrast with the 85% of legal nectar visits but agrees well with the 52% of pollen collected from these flowers as described above. Garden plants with

Table 10. *Number of visits paid to artificial flowers of different colours*

	Colour of flower					
	Red	Violet	Blue	Orange	Yellow	White
lucorum	9	13	15	33	32	12
pratorum	76	153	109	98	128	91
agrorum	14	10	7	12	19	6
Total	99	176	131	143	179	109

flowers in both colour groups have been omitted in these calculations. On the face of it, then, differences in colour preferences between species of bumble-bees seem very unlikely but some experiments were carried out with artificial flowers nevertheless. Although all the bees were foraging on natural flowers as well, and therefore already conditioned to certain colours, it was thought that any striking differences in preferences between the species would be apparent.

Six paper flowers were set out at the feeding place, all identical except for their colour, red, violet, blue, orange, yellow and white (it is not known whether ultra-violet was reflected or not). At least fourteen *pratorum* workers visited the 'flowers' but only three *lucorum* and three or four *agrorum*. The 'flowers' were watched for observation periods of at least one hour on fourteen days in June, July and August in 1953. During observation periods the 'flowers' were frequently interchanged and constantly replenished with syrup; between observation periods they were interchanged and replenished at intervals. The combined results are given in Table 10 and the difference between species is highly significant ($\chi^2 = 39{\cdot}3$, d.f. $= 10$, $P<1\%$). In view, however, of the very few individuals of two of the species not much importance can be attached to this. The behaviour of individuals is of more interest.

Pratorum workers *en masse* show the same preferences for blue with violet and yellow as the honey-bee and one or other of these colours received the greatest number of visits in each observation period. Nevertheless some individual *pratorum* workers were showing preferences for orange and yellow or for red. Details for the six marked workers who came regularly to the 'flowers' are given in Table 11 and the differences are highly significant ($\chi^2 = 47{\cdot}8$, $P<1\%$, d.f. $=8$, the colours have been grouped thus, red and white, violet and blue, orange and yellow, to obtain sufficient numbers to test). Four of these marked bees were seen at various times on flowers nearby as shown in the table and of these bee 3 and more particularly bee 4 were visiting natural flowers of a different colour from the artificial flowers that they 'preferred'.

Individual differences were noted in *agrorum* too, one bee visited mainly red, another paid fourteen visits to orange and yellow with only one visit to another colour in an hour. At the same time this bee was visiting yellow *Sedum* and pink *Chamaenerion angustifolium* (L.). Perhaps the fact that the 'flowers' were nearer to the *Sedum* in height accounts for the large number of visits to orange and yellow

Table 11. *Number of visits paid by six* pratorum *workers to artificial flowers of different colours*

Bee No.	Colour of flower						Natural flowers visited
	Red	Violet	Blue	Orange	Yellow	White	
1	7	3	2	2	3	5	Not seen
2	2	10	1	2	1	6	*Lavandula, Lupinus, Digitalis*
3	1	9	6	15	14	5	*Campanula carpatica* (purple), *Trifolium repens*
4	–	4	2	9	8	2	*Campanula carpatica* (purple), *Digitalis*
5	3	15	12	3	5	5	Not seen
6	7	1	1	4	–	2	*Lavandula*

though the bee must have been conditioned to the colour of *Chamaenerion* as well. Nothing was known of the normal foraging of the three *lucorum* individuals; one of these had a very decided preference for orange and yellow which it maintained for ten days, another had a similar preference at first but later visited all colours indiscriminately as did the third.

It seems likely from these results that the bees tended to become conditioned to a particular colour among the artificial flowers without much reference to other foraging experience, as a result perhaps of their first few visits which might have occurred when the 'flowers' were not moved much and some had dried up between observation periods. But if they can be conditioned so easily innate preferences can scarcely have much effect on their choice of flower colour in the field. To establish the matter beyond doubt experiments would have to be done on large numbers of individual bees.

Both *agrorum* and *pratorum* mix the colours of flowers visited on any one trip freely. Among sixty-four mixed pollen loads collected by *agrorum* and sub-

sequently identified (Brian 1952) forty-one contained mixtures of pollen from flowers of the red, violet, blue colour group with pollen from white or yellow flowers, seventeen mixed only the red, blue group and six the white, yellow group, thirteen mixed pollen loads collected by *pratorum* were analysed and seven, again more than half, mixed the two colour groups. The same thing has been noted in the honey-bee (Betts 1920).

The absence of different preferences between groups of pollinating insects, discussed by Kugler (1952), and between species of one genus, discussed here, does not necessarily mean, however, that colour preferences, or rather the type of colour vision of bees as a group has not influenced the evolution of colour in flowers, as Kugler suggests. Beale, Price and Sturgess (1942) from a survey of the distribution of different anthocyanins in flowers find a higher proportion of pelargonidin plants in the tropics and delphinidin and cyanidin plants in temperate regions. They point out that this must arise because natural selection favours the survival of red rather than blue flowered forms in the tropics since even tropical flowers

Table 12. *Competition and attraction on artificial flowers.*

The figures show the number of visits to occupied: and unoccupied flowers.

	Species of incoming bee	Total no. of 'flowers'	Number of flowers already occupied			
			1	2	3	4
1953	*pratorum*	5	69:126	23:39	6:10	1:5
			<·001%	8·6%	12·0%	2·0%
1953	*agrorum*	5	16:5	3:4	4:1	
			<·001%	29%	26%	
1953	*lucorum*	5	7:16	1:6		
			8·8%	13%		
1952	*pratorum* and *lucorum*	7	9:16	11:7	3:2	
			0·43%	0·31%	26%	
1952	*pratorum* and *lucorum*	4	7:7	2:1		
			2·8%	37·5%		

containing cyanidin or delphinidin derivatives are redder than temperate flowers which contain the same anthocyanin. They do not enlarge on how natural selection brings this about but it must surely be through the different pollinators in the two regions. In temperate climates the pollinators are mainly the red-blind bees, but in the tropics the importance of birds as pollinators may be even greater than that of insects (Grant 1953) and birds can see red and are more sensitive to it than to blue or violet.

COMPETITION AND ATTRACTION

(*a*) *On artificial flowers*

It has already been mentioned that when the artificial flowers were first set out in the garden bees were slow to find them, but that once a few had been introduced to them others came more readily, and this suggests that they were influenced by

the presence of other bumble-bees. Regular visitors to the 'flowers' were also influenced by the presence of other bees, an incoming bee often landing directly on top of a bee already drinking. On several occasions the behaviour of the incoming bee and the number of 'flowers' already occupied (by one or more bees) at the time was recorded. The results are set out in Table 12 and give the combined totals for several days in 1953 for each species separately and results for two days in 1952 for *pratorum* and *lucorum* jointly; the species of the occupying bee varied. Unfortunately the 'flowers' were not always all the same since the experiments were not always designed to demonstrate attraction, but the behaviour of the bees usually left no doubt that they were being influenced by the other bees. To test the significance of the results each record of behaviour can be regarded as a Bernoulli Trial, that is independent and with a probability of landing on another bee equal to the proportion of 'flowers' occupied at the trial. On this assumption the probability of obtaining k attacks in n trials is given by the term of the Binomial Theorem $\binom{n}{k} p^k q^{n-k}$ where p is the proportion of occupied 'flowers' and q of unoccupied. In Table 12 the probability is given in each case below the number of visits. It will be seen that, with the exception of *lucorum* in 1953, whose records were almost entirely from one individual, when only one 'flower' was occupied the incoming bee was strongly attracted to that 'flower'; this is comparable to the attraction between honey-bees under rather similar circumstances (Kalmus 1953). However, when two or three 'flowers' were occupied there was no attraction, except in one case, and for the only set of data where four 'flowers' were occupied the incoming bee actually avoided occupied 'flowers'. The meaning of this behaviour is not clear and without more data should not be stressed, but if it restricts the number of foragers on a given crop it will obviously be advantageous as would the attraction exerted by a single forager who has found a new crop. To bumble-bees, without the means of communication of profitable crops to nestmates, this latter behaviour would be particularly advantageous.

The behaviour of both incomer and occupant varied. When both bees were on the same 'flower' the incomer would either land quietly beside the bee in possession and begin to drink, or it would come down right on top of the other bee's back obviously trying to knock it off, after which it might or might not settle down to drink. The bee in possession was often disturbed and left even when not directly attacked, but if it stood its ground it would hold up one or two legs as though warding off the attacker; this attitude is frequently adopted in the nest when a bee is interfered with.

The general degree of aggressiveness of incoming bees was by no means always the same, but on days when strong aggression was being shown it seemed to have definite inter-species significance. For example on 30 May 1952 in $2\frac{1}{2}$ h a *pratorum* came in twenty times when a *lucorum* was already there and on thirteen of these occasions attacked, ten times dislodging the *lucorum*. In the same period a *pratorum* came in eight times when another *pratorum* was there and never attacked.

The general picture of inter-species relationships appeared to be as follows: *pratorum* is definitely aggressive towards other species, its attacks having an effect

on *agrorum* but little on *lucorum*; *lucorum* is least affected by aggressiveness in other bees (comparable to the position of the top hen in a peck order) and *agrorum* is only moderately aggressive under normal conditions, aggressiveness increasing as a result of attacks by other bees and, unlike the other two species, actually being kept away by the other bees. The behaviour of *hortorum* in this respect is not known.

An outline of the behaviour of *agrorum* in 1953 may illustrate this. On 17 July when the 'flowers' were first set out two *agrorum* and one *lucorum* were visiting them regularly. While they were being watched an *agrorum* came in twelve times when another *agrorum* was there and never landed on it, once an *agrorum* came in when a *lucorum* was there, hovered over it, moved away and then returned and landed directly on its back, failed to dislodge it and went right away.

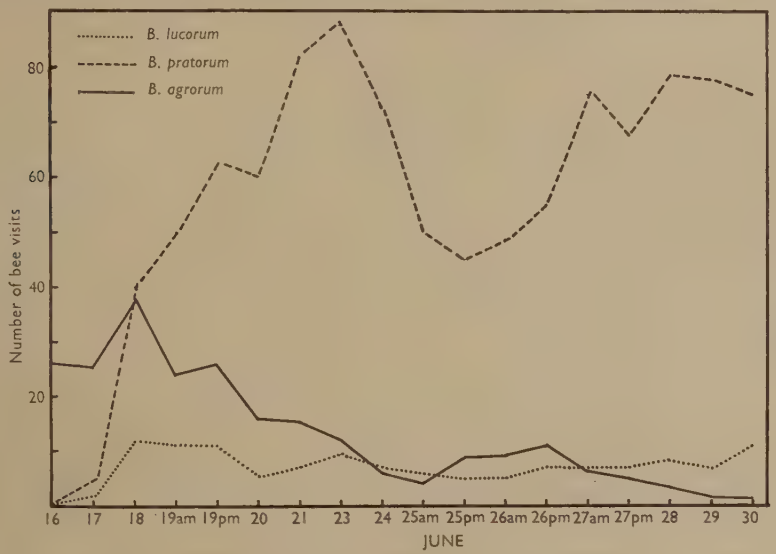

Fig. 3. Number of visits paid by bees of different species to artificial flowers in 1953.

On 18 June about three *agrorum* were paying regular visits and one *pratorum* had found the 'flowers'. On the next day antagonism was seen; on one occasion a *pratorum* attacked an *agrorum* while it was drinking, and having disturbed it the *pratorum* flew up and attacked it in the air, knocking it to the ground. The following day it drizzled and a noticeable absence of antagonism was recorded. By 24 June there was a definite change in the *agrorum* behaviour, they were no longer interested in the syrup but paid numerous visits to the 'flowers', when if another bee was present they would attack, but if no bee was present they left the 'flowers' untouched. By 28 June lack of antagonism was again recorded but on that day only three feeding visits by *agrorum* were seen compared with fifty-three by *pratorum*. By 30 June the 'battle' appeared to be over and twice *agrorum* were seen hovering over a drinking *pratorum* and failing to attack. On 1 July all the *pra-*

torum visiting the 'flowers', fourteen in all, were caught and caged for one day, but the *agrorum* behaviour (occasional inspections only) remained unchanged. On 11 August another *agrorum* was trained to the 'flowers' in another part of the garden. This bee had them to itself and visited them regularly, which indicates that it was not any growing lack of interest in syrup that led to the behaviour of *agrorum* described above; persecution by *pratorum* seems a more likely cause.

The total number of visits with drinking are shown as running averages of three observation periods in Fig. 3 for the bees of each species. This demonstrates the drop in number of *agrorum* visits as *pratorum* visits increase, although *agrorum* was known to still have an interest in the 'flowers'. Only one *lucorum* was involved and it kept up a fairly steady rate of visiting, apparently uninfluenced by the *pratorum*. The daily totals for *lucorum* and *pratorum* in 1952 fluctuated together which again indicates that the two species are indifferent to each other.

(*b*) *On natural flowers*

In 1952 it was noticed, while counting queens on half a dozen black currant (*Ribes nigra*) bushes, that while before 12 April twenty *lucorum* and seventeen *pratorum* but only one *agrorum* were seen, after this date, when only two *lucorum* and no *pratorum* visited the currant and very few were seen on any flowers at all (presumably because they were incubating their first pupae) eleven *agrorum* were then counted on the currants. Since *agrorum* had been seen frequently on other plants before, this suggested that competition was actually keeping *agrorum* away from the bushes.

In 1953 all contacts seen between bees on natural flowers were recorded—twenty-nine in all only. The records for *lucorum*, *pratorum* and *hortorum* are few so they have been combined to compare their behaviour with that of *agrorum*. As regards the behaviour of the incoming bee, six times an *agrorum* landed on or beside another *agrorum* but none was seen to land beside a bee of another species although five times they sheered off one in mid-air. Seven times a *lucorum*, *pratorum* or *hortorum* landed on or beside a bee of its own species, and eleven times on a bee of another species and they were never seen to sheer off. This certainly suggests that *agrorum* is less aggressive in the field. As regards the behaviour of the *agrorum* by or on which another bee landed, six times the incoming bee was another *agrorum* and the resident was never disturbed, but out of seven occasions when the incoming bee was of another species the *agrorum* was disturbed and left six times.

The observations on natural flowers thus reinforce the conclusions drawn from experiments with artificial flowers, namely that the species differ both in their aggressiveness and in their sensitivity to attack. They also suggest that the species recognize each other and though of course scent, which in the nest at least is distinct even to man, may play its part, it may well be that the well-marked colour patterns of the bees are of importance in this connection.

The fact that so few contacts between bees were observed in the field does not

mean that competition between species is unimportant, for the majority of bees seen on flowers are already experienced foragers and contacts would be expected to be most frequent between new foragers which have not already learnt to avoid (in the case of *agrorum*) flowers or areas frequented by other species.

DISCUSSION

Of all the factors examined which might influence the species of bumble-bees differently in their choice of flowers four have been found to be of importance: length of corolla tube, provision of nectar as well as pollen, habitat frequented and interactions between species. These have been investigated separately but it is probable that their interactions are of importance too. For example, *agrorum* may forage in exposed situations on particularly favourable crops such as red clover, or might visit more short-corolla-tubed flowers in the absence of *pratorum*. Harrison (1939) indeed records numerous *hortorum* queens visiting *Acer pseudoplatanus* in the Isle of Coll, but at Colgrain these trees were visited only by *lucorum* and *pratorum* neither of which species occurs on Coll.

Obviously therefore in any area the differences between species will vary according to the flowers available and the habitat type as well as the other species of bee present. Pittioni (1940) has given examples of this, for instance plants that are visited in the mountains but not in the plains. The lists of flowers visited published by many authors (see Brian 1954) show numerous discrepancies when compared one with another; for example in some areas *lucorum* visits *Digitalis purpurea*, in others as at Colgrain it does not. Because of this Kugler (1943) doubts whether any consistent differences in choice of flower exist between the species, other than those arising from structural, i.e. tongue-length differences. It seems more probable, however, that the differences are in fact consistent for any one place. They appear to arise not only from structural but also from psychological and physiological differences between the species; no evidence for innate preferences for certain plants has been found though it is possible they might exist in the very specialized *hortorum*.

In the Colgrain area studied no two species occupy exactly the same feeding niche. *Lucorum* stands out as a feeder in open spaces and trees, on open flowers — an opportunist as far as nectar collection goes visiting aphids for honeydew and biting holes in flowers, taking full advantage of the extra amount of pollen produced by many nectarless flowers and uninfluenced by the presence of bees of other species. It probably owes its greater abundance, and possibly in the long run its larger colonies, to these versatile foraging methods. It is favoured by man's activities, which create open pasture and heather moor, more than the other species, though this must be offset to some extent by competition with honey-bees with a tongue only 1 mm shorter. *Hortorum* at the other extreme is a very specialized bee, strongly influenced by the length of its tongue and restricting itself to flowers too long for other bees. Coupled with this it seems to be conservative, unadapted psychologically for the collection of pollen alone or for

nectar robbing; indeed it is hard to imagine how the long tongue could have been evolved were this not so. Its habitat preference or relations with the other species is not known.

The other two species with tongues of intermediate length, *pratorum* and *agrorum*, are similar to each other and different from *lucorum* in habitat choice and restricted specialization for pollen collection, but one is aggressive, the other more retiring. Both, one might suppose, can live in the same area partly through a slight tongue length difference but perhaps even more through a temporal difference; *pratorum* is common earlier in the year, *agrorum* later. The position may be diagrammatically described as shown in Fig. 4; in a more natural habitat the species might be much more ecologically distinct.

Some of the different behavioural characteristics of the species are not perhaps

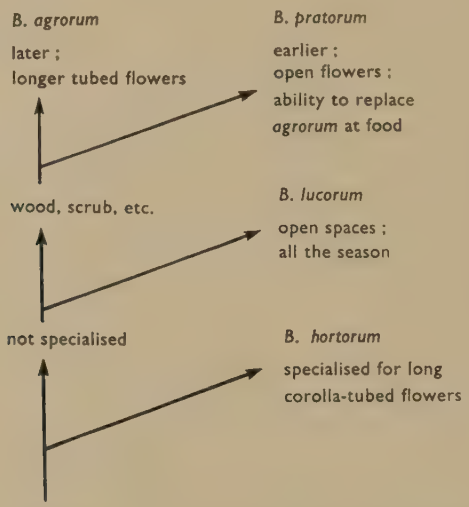

Fig. 4. Diagram to represent the ecological relationships between the species of *Bombus*.

as disconnected as they appear, and the following theory connecting them may be put forward tentatively. The main drive of the foraging bee is usually assumed to be directed to the collection of nectar, though this is probably an over simplification. If the nectar is inaccessible the nectar collecting drive will be blocked and random biting of the tissue of the flower may occur. Originally this biting may have been simply a displacement reaction, but since it can result in making the nectar accessible it would acquire survival value and be incorporated in the behaviour pattern of the foraging bee. But biting is definitely an aggressive act; it is the main method of fighting between worker bumble-bees and is also used in defence of the nest. One might suppose therefore that differences in the threshold of aggression between the species would parallel differences in their readiness to bite flowers and this probably is the case. *Lucorum* and *pratorum* have been shown

to be more aggressive at artificial nectar sources than *agrorum*; furthermore *lucorum* workers are more aggressive in defence of their nest than *agrorum* and correspondingly *lucorum* is one of the chief biters of flowers.

This hypothesis can be extended to include the deliberate collection of pollen as opposed to incidental collection when the bee becomes dusted with pollen while collecting nectar. This usually involves biting and pulling at the stamens with the mandibles and this behaviour may also have originated as a displacement activity when the stamens have blocked the way to the nectar or no nectar was present. A clear example of this was observed when an *agrorum* queen visiting a garden *Iris* of the bearded type tried two or three times to push its head into the flower, failed and then tore at the stamens with its mandibles several times without attempting to collect pollen before flying away. In this case, too, the species with the lowest threshold of aggression, *lucorum* and *pratorum*, would be expected to be the species found biting anthers and collecting pollen deliberately most often—as has been shown to be the case. It thus seems possible to derive several of the foraging behaviour traits which have been shown to characterize a species from the level of the threshold of aggression. It is possible even that tongue-length differences between species of *Bombus* arose from the same cause, for it is doubtful whether the extra long tongue of *agrorum* or *hortorum* really confers any advantage to the species over the shorter tongued bumble-bees. Rather it may be that in the mutual evolution of very long-corolla-tubed flowers and very long-tongued bees, only those species of bumble-bees took part which were psychologically unadapted to obtain nectar from these flowers in other ways; the other species retained the more adaptable tongue of medium length.

SUMMARY

1. The feeding plants of queens and workers of *Bombus lucorum*, *B. pratorum*, *B. agrorum* and *B. hortorum* in a small area in west Scotland were assessed by counts of foraging bees made during three seasons and showed a partial division of the bee flora between the four species.

2. Seven of the factors which might lead to this division were investigated, either in the field or by experiments with artificial flowers visited by free-flying bees.

3. To three of these factors: colour, general shape and height of flower above the ground, the species reacted in the same way. To two other factors: presence or absence of nectar and degree of exposure of habitat, they responded differently, while competition between species also had a differential effect. All species are affected by the length relationship between tongue and corolla tube, but all pay most visits to flowers with a corolla tube considerably shorter than their tongue.

4. The differences between the species were as follows: *lucorum* visits open flowers, collects honeydew and 'steals' nectar, forages in exposed habitats, collects pollen without nectar and is relatively uninfluenced by the presence of bees of other species. *Hortorum* is restricted to long-corolla-tubed flowers and unadapted psychologically for collecting pollen without nectar or for stealing. *Pratorum*

visits mainly open flowers, forages in sheltered habitats, and is aggressive to other species. *Agrorum* visits flowers of intermediate corolla-tube length, forages in sheltered habitats later in the season than *pratorum*, and is retiring in its behaviour to other species.

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A STUDY OF A POPULATION OF THE LEECH *GLOSSIPHONIA COMPLANATA* (L.)

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(With 6 Figures in the Text)

INTRODUCTION

Glossiphonia complanata is a leech which often occurs abundantly in running water with a high calcium content. An investigation of its life history was made in a chalk stream carrying water from the Kimber Head Springs to the River Pang at Stanford Dingley, Berkshire (National Grid reference 583715). The water is used to irrigate watercress beds, and in the outflow channels of the watercress beds *Glossiphonia* is sufficiently abundant to make regular sampling possible.

A previous investigation (Mann 1953) had been made into the life history of *Erpobdella octoculata* (L.), and it was thought that the life history of *Glossiphonia complanata* would make an interesting comparison on account of the contrasting structure and habits of the two species. *Erpobdella* is long and narrow and rounded in cross section. It lacks proboscis or teeth and swallows its food whole, devouring chironomids, oligochaetes, etc. *Glossiphonia*, on the other hand, is relatively short and broad, and flattened dorso-ventrally. It is armed with a proboscis, which it inserts into the soft parts of invertebrates, especially gastropods such as *Hydrobia jenkinsi* Smith and sucks out their body fluids. It has been shown (Mann 1955) that both leeches are found most abundantly in streams, but *Erpobdella* is characteristic of soft water, and *Glossiphonia* of hard. *Erpobdella* produces a cocoon with a hard outer covering. This it cements to a stone or other solid object and abandons, but *Glossiphonia* produces a cocoon with a soft transparent covering, which it broods over, covering it with its body. The young, on hatching, become attached to the ventral side of the parent and are carried about for some time. Both species are to be found attached to the undersides of stones at all times of the year, so that comparable results were to be expected from regular samples collected by the simple process of removing all leeches encountered while turning all the stones of more than 5 cm diameter in a selected area of the stream bed.

METHODS

Sampling was carried out at monthly intervals from August 1953 to July 1954, with the exception of December and February, when flooding made accurate sampling impossible. Further observations were made between March and June

1955. About 100 leeches were collected, weighed individually, and returned to the stream. For the first six months the sampling was confined to the stretch of stream marked AB in Fig. 1, but the flooding of February 1954 altered the nature of the bottom, and it was not possible to find sufficient leeches within the limits A-B. Presumably the current had swept downstream many of the suitable stones, and the leeches with them. It then became necessary to collect along the stretch marked C to I (Fig. 1). This resulted in a slight discontinuity in the records, but the main trends remained clearly discernible. All the 1955 observations were made along the stretch C to I.

Weighing was carried out on a direct-reading, air-damped balance, the leeches being weighed alive after drying surface moisture on filter paper. The weights were read to the nearest 0·1 mg and grouped in 2 mg classes. Leeches showing full gonads and those brooding over eggs or young were recorded separately. The latter were weighed complete with brood.

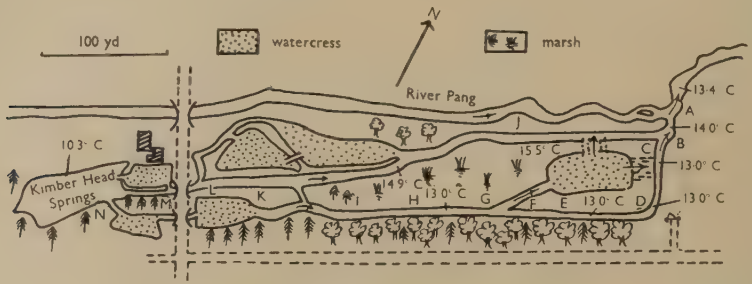

Fig. 1. Sketch-map of the collecting area. Temperatures were recorded at 2 p.m. on a sunny day in May. For explanation of lettering see text.

From March till July 1954 counts were made of the percentage of individuals with eggs or young, at intervals of 5 to 7 days. At first these counts were restricted to the area C-D (Fig. 1) in order to minimize variation due to differing conditions along the length of the stream, but once again difficulties arose because it was found that after the leeches had been disturbed they rolled into a ball and were carried downstream, and after a few counts on the same stretch the number of leeches present began to decline markedly. The area of investigation was then considerably widened, and this led to the discovery of a correlation between breeding activity and the temperature of the water in various parts of the stream.

RESULTS

Fig. 2 shows the unsmoothed frequency polygons of the weights of the leeches in the samples, in 2 mg classes, at monthly intervals between August 1953 and July 1954, except for December and February when samples were not obtained. If we assume that the pattern of change reflected in the graphs is repeated annually we may follow the history of a year-group several times through the cycle,

and construct a picture of the entire life history. Comparing the May with the April sample, we see that about 6% of the population lies between 0 and 6 mg, and is present in May for the first time. More small specimens are added to the population in June, and in July about 19% of the population is made up of new recruits weighing up to 12 mg. The corresponding group in August lies between 0 and 18 mg and a marked bimodality is evident. The same group can be followed

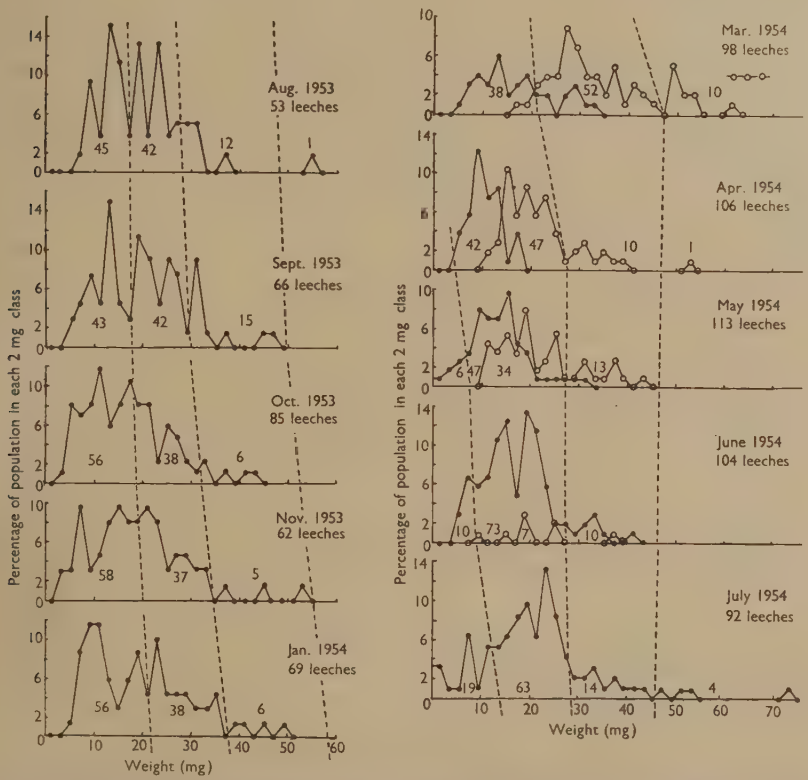

Fig. 2. Unsmoothed frequency polygons representing the distribution of the weights of leeches in 2 mg classes in ten samples taken between August 1953 and July 1954. Leeches with eggs or young are recorded separately. Dotted lines suggest divisions between year-groups; figures refer to the percentage of the population in each year-group or brood.

through the autumn samples, with evidence of further recruiting in the lower weight classes. By January the weight limits are 4 to 20 mg, and in March it seems probable that the same group is represented by the immature leeches below 24 mg. In April rather more than half of this group are breeding. This means that many of them will be weighed with young attached to the ventral surface, and there is an increase in the amount of water carried on to the balance. It is therefore reasonable to extend the upper limit of the age-group, and to include all those

up to 28 mg. In May a proportion of the smaller leeches in the age-group is breeding, but many others never become mature, and breeding activity shows a marked decline in June, and is finished in July. There is a fall in weight when the breeding leeches release their young. The bimodality of the one-year-olds is clearly shown at this time, and the two peaks of this group may be followed through the autumn and winter samples, but the heavier component shows a decline in numbers in October to January, suggesting that those leeches which produced a brood are suffering a heavier mortality than those which did not. The limits of the group, now approaching two years of age, is 20 to 38 mg in January, with the upper limit rising to 46 mg in March when they are being weighed with their broods. In the following months the two-year-olds are scarce compared with the one-year-olds, showing that heavy mortality has occurred. Even so, a few individuals may be traced through the life cycle a third or even a fourth time, although the only suggestion of a four-year-old is a single large individual found in each of two samples.

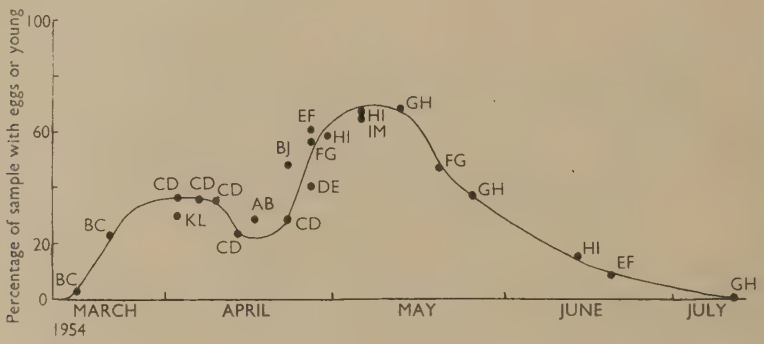

Fig. 3. Proportion of leeches with eggs or young during the breeding season. Places of sampling indicated by letters referring to Fig. 1.

Fig. 3 shows the percentage of leeches brooding over eggs or young, at intervals of a few days from March to July. As has been explained, the process of counting resulted in a downstream movement, so that successive counts had to be made in different parts of the stream to avoid displacement of the population. The general trend of the points suggests that there are two broods produced in the season, a March-April brood, and a May-June brood. Comparison with the results of weight sampling shows that the first brood is produced by the two-year-olds, and the second by the one-year-olds. Each period of activity lasts about 20 days, and this agrees well with the course of events observed on individuals breeding in the laboratory, which was as follows. The eggs were laid in two or three gelatinous capsules and attached to a stone. They were brooded over by the parent for 5 to 6 days, after which the embryos hatched and became attached by the ventral side of the head to the ventral surface of the parent. At about ten days after egg-laying, at a length of about 1·5 mm and weight of 0·3 mg the young lost

their attachment by the head, and became attached by the posterior sucker. The time at which they finally left the shelter of the parent's body varied between 14 and 24 days after egg-laying.

The scatter of points about the line in Fig. 3 presented a problem until it was noticed that temperature conditions varied from place to place in the stream. It then appeared that the counts made in the warmer water showed an advance in breeding time, and those made in the colder water showed that breeding was retarded. The temperature conditions at 2 p.m. on a sunny day in May are indicated in Fig. 1, but the general picture obtained by making a large number of observations at different times of day is as follows. The temperature of the water from the Kimber Head springs was fairly constant at 10-11° C. The water passing along the stream I-H-G-F-E-D was heavily shaded from the sun and the diurnal rise in temperature was never more than 3° C. The water passing along L-K-J-C was in full sun and received water from the watercress beds, and the diurnal rise was 5-6° C. That time of breeding may be related to this difference may be seen from the fact that on 22 April 48% were breeding at B-J and only 28% at C-D. On 2 April 36% were breeding at C-D but only 28% at K-L which is closer to the springs, and so on. Conditions along the length of the southern, shaded stream were found to be fairly uniform, and after 26 April samples were taken only from this region. Even so, another source of error became apparent. It was found that where the stones were abundant and the leech population dense, the percentage breeding was much higher than in places where the population was less dense. For instance, in the region H-F it was estimated that the density of leeches was about five times higher under the north bank than under the south, and the proportion breeding on 5 May was 76% for the dense, and 26% for the less dense population. Several instances of this kind were found, and the samples recorded on Fig. 3 were taken so as to include dense and less dense populations in the proportion in which they occurred in nature.

The interpretation of the life history given previously hinges on the sequence of events during the breeding season, so observations were repeated along the stretch G-I during the breeding season of 1955, and the opportunity was taken to obtain additional information about the temperature at which breeding commenced, and about changes in density of the population. As before, the two-year-olds started breeding about a month before the one-year-olds, but the former began about two weeks later than in 1954. In 1954 the proportion of one-year-olds with eggs or young rose to a maximum of over 60%, but in 1955 this figure was never above 50%. These differences are probably explained by the cold, dull weather experienced at the time. (The author understands that the sequence of events in the plankton of Windermere was also about two weeks later than usual.)

Maximum and minimum thermometers were placed in the stream and read twice a week. On the day when the first eggs were seen the minimum temperature reading was 8·8° C and the maximum 11·7° C. The next readings were lower, 7·4° C and 11·5° C, but after that they climbed steadily over a period of four weeks

to a level where the maximum was 14-15° C and the minimum about 8° C, and this temperature was maintained throughout the breeding season.

Estimates of density were made on four occasions. The bed of the stream consisted of a layer of coarse gravel (particle size 0-2 cm) and stones (greatest diameter 10-25 cm) scattered irregularly over the gravel. The density of the leeches in the gravel was estimated by throwing quadrats 25 cm square at random and counting the number of leeches enclosed and the number breeding. The density of the leeches on the stones was obtained by using a sheet of perspex 25 cm square and a glass pencil. As each stone was examined for leeches its outline was marked on the perspex, and the process continued until the outlines of all the stones examined, when fitted together in the most economical way, just filled the square. Details of the first and the last set of observations are shown in Table 1. An analysis of variance shows that there was a significant fall in density of the population between 15 April and 27 May, and that there was a significantly higher density on the stones compared with the gravel. This confirms the conclusion

Table 1. *Numbers of leeches in each quadrat of* 25×25 *cm*^{2} *on two separate occasions. For method of sampling see text*

15 April		27 May	
Gravel	Stones	Gravel	Stones
11	13	10	16
14	34	4	17
16	42	0	13
4	27	4	15
45	116	18	61

The difference between gravel and stones is significant at the 1% level of probability, and the difference between dates is significant at 2%.

reached from the analysis of age structure of the population before and after breeding, that there was a heavy mortality of two-year-old leeches.

A separate record was kept of those breeding and those not breeding, on each stone examined. On 15 April 33% of all the leeches on the stones were breeding. In Fig. 4 this fact is represented by the line A which makes with the x axis an angle whose tangent is 0·33. It is seen that on 15 April the points representing counts on the individual stones are distributed evenly about the line. On 3 May, however, the points are not evenly distributed about the line of the mean, as those stones with the larger number of leeches had an above-average proportion of breeding specimens. On the other two occasions when such counts were made, the numbers breeding were too small to show any distinct trend. On 15 April the first brood had passed its maximum; on 3 May the second breeding period was beginning. In 1954 it had been noticed that a more dense population had a higher proportion of breeding specimens, and the explanation which best fits the facts is that when a particular year-group begins to breed, those leeches which are

aggregated more densely carry out cross-fertilization sooner, and deposit their cocoons sooner, but that after breeding has been going on for a week or two the leeches in the less dense aggregations have been fertilized and no difference is apparent.

Breeding leeches were taken from the first and second broods, and their young were removed and weighed. The mean weight of 222 young from the first brood was 0·31 mg and the mean of 95 from the second brood was 0·24 mg. This difference may be related to the fact that the parents of the second brood are younger, smaller leeches.

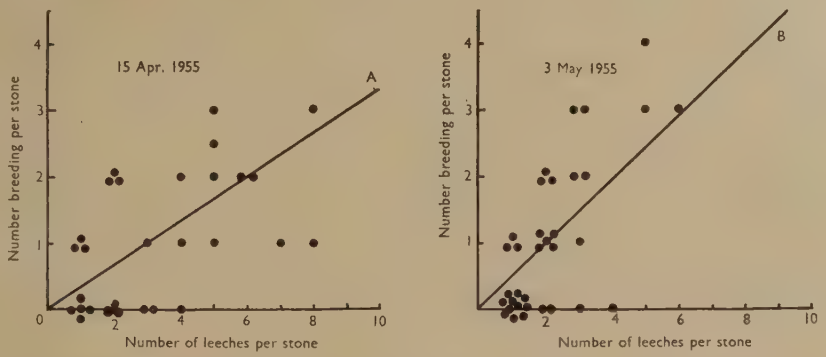

Fig. 4. Graphs showing the relationship between the number of leeches under a stone and the number breeding. The lines are drawn to represent the average figure for all the stones examined on that day.

DISCUSSION

(*a*) *Life history*

The outline of the life history of *Glossiphonia complanata* is surprisingly similar to that of *Erpobdella octoculata* described in an earlier paper (Mann 1953). Both breed for the first time at one year of age, and for a second time at two years of age. In both species a small proportion of the population lives and breeds in the third year, but in *Glossiphonia* it is possible that a few individuals live to four years. In both species the two-year-olds breed earlier in the year than the one-year-olds, and the young of any particular year are produced in two broods. In *Glossiphonia* there is an interval of time between the liberation of the young and their appearance in the population on the stones. Presumably this is spent in the gravel between the stones, and it appears that the migration on to the stones occurs at about 4-6 mg weight. Two such migrations may be traced on the frequency polygons, a peak at 4-6 mg which first appears in the June sample, and another peak at 4-6 mg which first appears in the October sample. These presumably correspond with the two broods represented in Fig. 2, but whereas the two broods were separated by only 5 weeks, the migrations on to the stones were separated by 4 months. It

is suggested that the second brood which is smaller at hatching, being the offspring of smaller parents, take longer to reach the weight of 4-6 mg at which migration occurs.

The effect of the two periods of recruitment into the population is to make the year-group bimodal from October onwards, and when the one-year-olds begin to breed the heavier component becomes mature earlier than the lighter component. Moreover only 40% of the lighter component reaches maturity in the first year of life. A similar explanation was put forward for the bimodality of the year-groups in samples of *Erpobdella* (Mann 1953). An alternative explanation has been put forward and is worth discussing. It is, that a difference in age of little more than a month is insufficient to account for the difference in weight of the two groups, and that there are two races involved, one tending to grow faster and to reproduce earlier than the other. The question of rate of growth is dealt with below, but if the hypothesis were true, the heavier component of both the one- and the two-year-olds ought to breed early, and the lighter components of the two-year groups ought to breed late. In other words there ought to be a stage at which, reading from left to right on the frequency polygons, there are immature one-year-olds, mature one-year-olds, immature two-year-olds, and mature two-year-olds. Since this stage has never been encountered, the hypothesis must be rejected. Also, since both the heavy and the light component of the two-year-olds were breeding at the same time in March, interbreeding will almost certainly have occurred, preventing the segregation of two distinct races.

(*b*) *Mortality*

The ratio of the 0+ year-group to the 1+ group is about 1·5 : 1 over the period October to January, suggesting that this is the stable condition between breeding cycles. If the population remains at the same density from year to year the mortality in a year-group between the ages of 6 months and 18 months is therefore such as to reduce three leeches to two, i.e. 33% per annum. The mortality between 18 months and 30 months is much higher, 83-88%, showing that two years is the normal span of life. It is clear from the frequency polygons that most of this mortality occurs immediately after breeding.

The number of eggs brooded by a leech varied from 5 to 70, with a mean of 33. The number of young carried varied from 17 to 38, with a mean of 26. The percentage of the population which breeds during the year may be estimated as follows. The composition of the population in October and January was: 0+ years, 56%; 1+, 38%; 2+, 6%; and since most of the mortality occurs after breeding, we may assume that the composition of the population is much the same during breeding as in January. In March all the 1+ and 2+ groups were breeding, totalling 44%. (The actual figure in the March sample was higher, but for reasons given earlier, is probably inaccurate.) The whole of the heavier component of the 0+ group appears to have bred either in April or May, and comprises half of the 0+ group, i.e. 28% of the total population. None of the lighter component of the

0+ group was breeding in April, but 40% were breeding in May. These represent 11·2% of the total population, and brings the total to 83·2%. Therefore for every 100 leeches present in January, about 83 bred during the year, and produced 83·2 × 33, *i.e.* 2746 eggs, of which 83·2 × 26, *i.e.* 2163, hatched and became attached to the ventral surface of the parent. The condition for the maintenance of the population at the same level is that the 2163 young should be reduced to 56 by the following October, and this implies a mortality of 97·4% in the first 6 months of life.

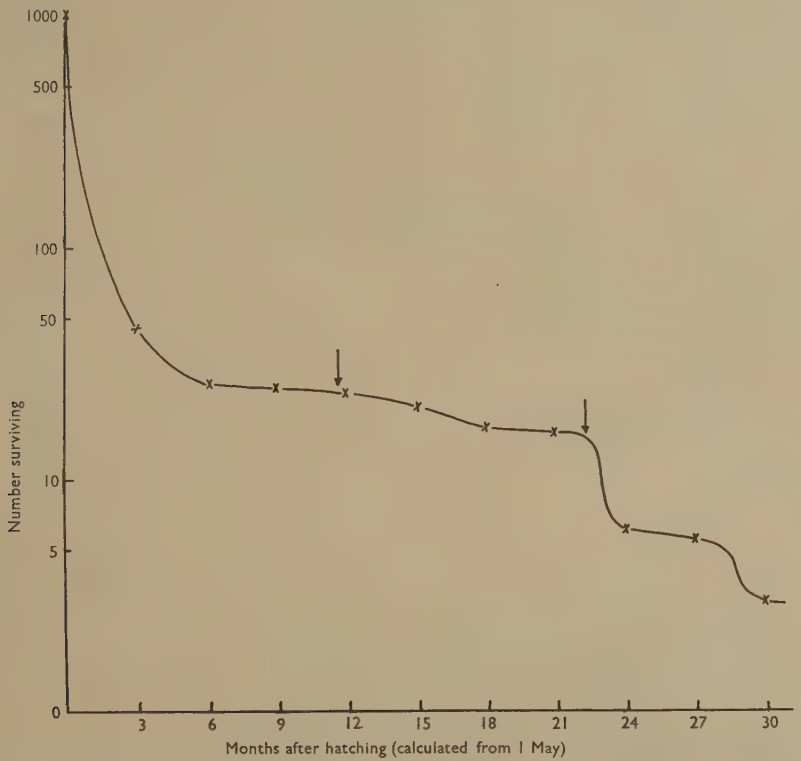

Fig. 5. Survival curve for 1000 newly hatched leeches calculated from the changes in the relative strengths of the year-groups in successive samples. Arrows indicate time of breeding.

There appears to be a higher rate of mortality in the heavier component of the one-year-olds during the autumn months, for whereas the two components seem to be present in equal numbers during breeding, the lighter component becomes relatively more abundant during October and November, and this shows well when the 1+ group is breeding in March. The differential mortality may reasonably be attributed to the differing proportions of individuals breeding in the previous spring. Using the mortality figures previously calculated, it is possible to plot a few points on a survival curve (Fig. 5). Starting with a hypothetical popu-

lation of 1000 newly hatched leeches on 1 May, the population is reduced to 26 by 1 October, to 17 a year later, and to 3 after a further year. The shape of the curve between these points has been calculated from changes in the relative numbers of each age-group in the samples. Clearly the times of heavy mortality are soon after hatching, and at the breeding season at two years of age. Mortality is also evident among the 1+ and 2+ age-groups in the autumn.

The survival curve appears to correspond most nearly with Pearl's (1940) 'positively skew rectangular curve', in which there is a heavy mortality in early life, but the survivors have a relatively high expectation of further life. Deevey (1947) drew attention to the scarcity of data illustrating this type of life history.

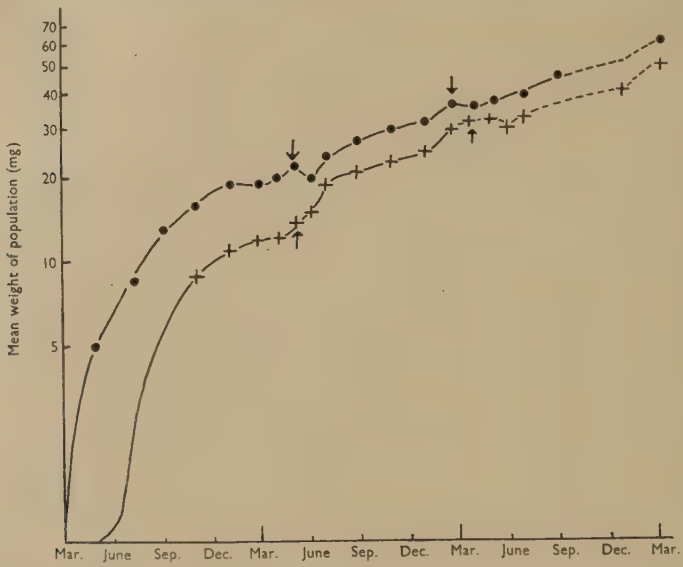

Fig. 6. The curves of log $n+1$, where n = mean weight of population in mg, plotted against time. Upper curve is for the earlier brood, and lower curve for the later brood. Arrows indicate time of breeding.

and although the details of this survival curve are only approximately correct, there is no doubt about the general shape. Deevey (1947) specifically mentioned that evidence from the age structure of a population is valid for the construction of a life table, provided one assumes that the population is stable.

(*c*) *Growth*

Fig. 6 shows the growth curves for the heavier and the lighter components of a year-group, calculated from the frequency polygons for weight distribution. The heavier component, resulting from the March brood, grows rapidly through the summer and autumn to a mean of 19 mg. Growth ceases in the period January-March and then there is a 2 mg increase in weight due to the animals being weighed with their broods, and therefore carrying over more water. There is a correspond-

ing drop when the young are released, after which the adults start another period of rapid growth and the annual cycle is repeated. The rate of growth in the second year of life is much less than in the first, and the total weight increment is only 13 mg in the second, compared with 19 mg in the first.

The lighter brood, resulting from the May-June breeding activity, is slow to join the adult population on the stones, but the points plotted from November onwards fit a curve drawn parallel to the curve for the earlier brood, but 6-7 weeks later in the season. According to Fig. 3 the two broods are separated in time by only four weeks, so it is clear that the second brood grows away less rapidly than the first. An explanation of this may perhaps be found in the fact that the second brood are from younger, smaller parents, and hatch at a smaller size, and that the second brood spend longer in the gravel before coming on to the stones, so that food may be less readily available to them. The growth check

Table 2. *Comparison of the life histories of* Glossiphonia complanata *and* Erpobdella octoculata

	G. complanata	*E. octoculata*
Breeding period	March-May	June-August
Average number of young per parent	26	23·5
Mortality in first 6-9 months of life	97%	91%
Proportion of year-group breeding at one year old	70% (lower in 1955)	87%
Mortality from 6 to 18 months	33%	49%
Proportion of year-group breeding at two years old	100%	100%
Mortality from 18 to 30 months	84-88%	69%
Proportion of total population surviving to three years	5-6%	4%

experienced when breeding is much less severe for the second brood, in which only 40% breed at one year of age than for the first brood, in which 100% breed at one year of age. This enables the second brood to reduce the weight difference between the two broods at the breeding season. In the summer and autumn of the second year of life the growth curves run parallel, and it is probable that they continue to do so for the third year. There is certainly no evidence for the suggestion mentioned earlier that there are two races present, which differ in their growth rates.

(*d*) *Comparison with* Erpobdella octoculata

A comparison of the life cycle of *Glossiphonia complanata* with that of *Erpobdella octoculata* has been made in Table 2. It is remarkable that two leeches differing so widely in structure and habits should have such similar life histories, even to the extent of both having bimodal year groups caused by the two-year-olds breeding a month earlier than the one-year-olds. The main differences are that *Glossiphonia*

has an earlier breeding season, and a lower proportion of the one-year-olds reaching maturity. This is accompanied by a lower mortality in the first year of life. On the other hand the mortality at two years seems to be higher, and the proportion of the population living to three years is only a little higher than for *Erpobdella*.

(*e*) *Factors governing the onset of breeding*

Among the factors governing the onset of reproductive activity, age is clearly important, for in 1954 all the leeches aged two or over bred, but only 70% of the one-year-olds bred. Also, of those that were fully twelve months old in April, *i.e.* the heavier component of the one-year-olds, 100% achieved maturity, but of those that were only 10-11 months old, only 40% achieved maturity. The correlation with size is not very close, for a specimen of only 8-10 mg was breeding in June, while many leeches of 12-14 mg failed to reproduce.

The fact that breeding was more advanced in the more dense population is not surprising. If environmental factors are favourable, and the gonads of an individual are ripe, the only stimulus needed to bring about cocoon deposition is the implantation of a spermatophore on the body surface by another leech. Clearly the chance of this happening is greater in a dense population than in a sparse one.

The environmental factors usually associated with the onset of breeding activity are an appropriate temperature and a suitable day length. The results already quoted suggest that leeches in that part of the stream where there is a marked rise in temperature during hours of sunlight begin to breed earlier than those in shaded parts, or close to the source of cold spring water, but more work is required to confirm this point, and investigate the quantitative relationship. It would be unwise to attempt this until the population has recovered from the disturbance involved in the present work.

ACKNOWLEDGMENTS

The author gratefully acknowledges his indebtedness to Professor A. Graham and Dr T. T. Macan who read and criticized the paper, Mr G. Williams who discussed the work in progress and advised on sampling methods, and Mr W. E. Stoneman who provided transport for the field work.

SUMMARY

1. The life history of *Glossiphonia complanata* was investigated by weighing individually all the leeches in samples taken from a tributary of the River Pang, Berkshire, between August 1953 and July 1954, and by further observations in 1955.

2. Assuming that the population is stable, the life history was found to be as follows. Eggs were laid in two distinct broods, the two-year-olds laying in March and the one-year-olds in April-May. The parents each produced an average of

26 young, over which they brooded for about 20 days. At one year of age 100% of the early brood were breeding, but only 40% of the late brood. At two years of age all were breeding, and most died soon after. A few survived to breed at three years of age (probably those which did not breed at one year), and an occasional specimen may have been four years old.

3. The mortality was 97% of the age-group up to the first October of life, 33% in the next 12 months, and 84-88% in the following 12 months. Only 5-6% of the total population were three years old or more.

4. The early brood and the late brood had differing mean weights throughout life. The rates of growth were comparable except that the late brood grew more slowly in the first few months of life, but faster during the first breeding season when many of them were immature.

5. There is some evidence that breeding begins earlier in those parts of the stream warmed by the sun, and in the more dense populations.

6. The outline of the life history is similar to that of *Erpobdella octoculata*.

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THE DISTRIBUTION OF *ASELLUS* IN WINDERMERE

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(With 2 Figures in the Text)

Many British freshwater animals are neglected because they are common, unspectacular and regarded as hardly worth consideration. *Asellus* is a case in point; but when a real study is made of the animal it is found that there is very little relevant information about its ecology, food and behaviour that would provide a basis for understanding its position within the ecological framework. *Asellus* has many advantages as an animal for intensive study. It is easily collected and identified, and there are only two species so far recorded from the surface waters of this country (Moon 1953), namely *Asellus aquaticus* (L.) and *A. meridianus* Rac. The third species, *A. cavaticus* Schiödte is a cave and well form. They can be obtained in large numbers in certain places and live and breed easily in the laboratory as experimental animals. It was reasons such as these which prompted an investigation of the ecology and distribution of *Asellus* in Windermere.

METHODS

The methods used in an ecological survey must be adjusted to the object in view. It is no use just imposing elaborate quantitative methods on a habitat and assuming that the results will automatically make sense. The environment is not a calculating machine, and too little is known about the behaviour and physiology of the animals living in the habitat.

In this case the facts were as follows. Preliminary collections had shown that two species of *Asellus* occurred in the lake, occupying the same types of habitat, and there was evidence to show that the distribution of the two species over the lake as a whole was not the same. The information required was concerned with the presence or absence of *Asellus*, and the proportions in which the two species occurred at different parts of the lake. It was with these points in view that the following methods were employed.

In the first 60 cm of the lake accessible for hand net collections a large stramin net was used, the stones being lifted and washed in the net while the substratum was stirred up and the debris netted. As a rough basis for comparison, collections were based on two minute intervals, experience having shown that if *Asellus* was common it would be discovered by a two minute collection. If, after three two minute collections in a particular place *Asellus* was not found, absence was pre-

sumed, although it is unwise to assume too readily that an animal is absent because it cannot be collected. The hand net collections were of two kinds. These were the random collections at stations spaced at frequent intervals around the shores, and the 'crawls' in which two minute collections were made at 50 m intervals or even closer along certain stretches of shore line. Some of the 'crawls' extended for about 1 km. In deeper water dredges were used, a sledge type with a bag between the runners for easy ground, and a heavy bag dredge for difficult ground. In certain places an Ekman grab of 0·05 sq. m capacity was used.

These methods served their purpose in that they made it possible to survey the whole lake. Detailed quantitative methods would have been too slow and as a

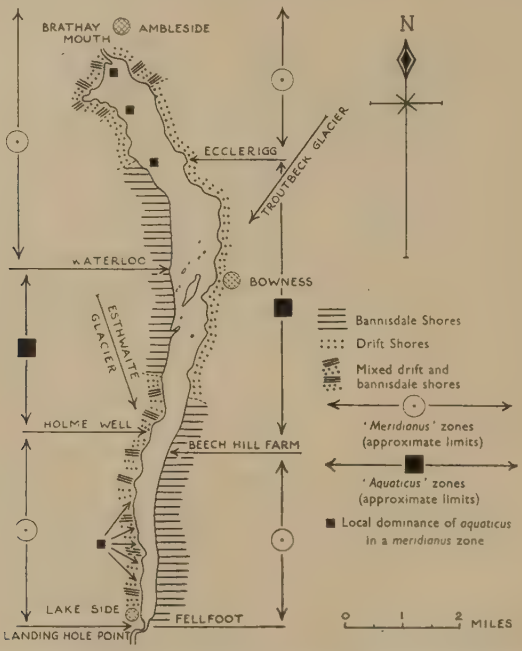

Fig. 1. The distribution of the two species of *Asellus* in Windermere (excluding the islands) in relation to the types of shoreline.

result of the smaller area covered would not have given a true picture of *Asellus* distribution. Furthermore it would have been impossible to devise a uniform quantitative method capable of working on the great variety of substratum encountered along the shore and down to a depth of 6 m. Even with this rough and ready method difficulties were frequent as, for example, a comparison of two minute collections in mud and leaves with two minutes in a difficult substratum of boulders and stones. There was also the problem of comparing dredge samples with hand net collections. Despite these difficulties the *Asellus* in the collections were counted as a rough guide to abundance and to the proportions of the two species.

Results based on the kind of methods described above must be based on a large number of collections from many stations, and the results discussed in this paper are based on 727 collections at 436 different stations in Windermere. Most of the collections were of necessity made in the summer months, but a number of shore collections of both types together with dredgings were made in the early spring with the water at its winter temperature of 4-5° C. The distribution was the same in winter as in summer, except that the winter forms were larger than the summer, a fact that is well known in *Asellus*.

Finally, it must be borne in mind that, in view of the present lack of detailed information concerning the behaviour and physiology of most of the freshwater invertebrates, it is unlikely that one will arrive at an adequate explanation for the distribution revealed by a survey. As far as *Asellus* was concerned the most one could hope for was the chance to make a few intelligent guesses.

Table 1. *Distribution of* Asellus *on the eastern and western shores of Windermere*

The numbers indicate the number of stations at which the two species occur.

	Asellus absent	*aquaticus* only	*meridianus* only	Both species present		
				Equal	*aquaticus* dominant	*meridianus* dominant
WESTERN SHORE						
Brathay Mouth to Waterloo	32	16	44	12	12	1
Waterloo to Holme Well	3	45	0	0	3	0
Holme Well to Landing Hole Point	6	8	19	7	2	0
EASTERN SHORE						
Brathay Mouth to Ecclerigg Bay	7	0	4	0	0	2
Ecclerigg Bay to Beech Hill Farm	4	31	0	1	2	0
Beech Hill Farm to Fell Foot	3	3	22	5	0	1

RESULTS

(*a*) *The hand net collections*

The general distribution of the two species along the shores of Windermere is given in Table 1 and Fig. 1, and it will be seen that the lake is divided into three zones. The north and south ends of the lake are dominated by *A. meridianus* whereas the middle region is predominantly *A. aquaticus*. It should be pointed out that the more frequent collecting on the western shores of the northern zone is due to two things: firstly, the northern zone on the east is very short owing to the fact that the middle zone runs so far north on the east side and there is no big indentation corresponding to Brathay Bay; secondly, two of the longest 'crawls' were

Table 2. *Typical 'crawl' collections*

Numbers of *Asellus* in 2 min collections at 50 m intervals
A, *A. aquaticus*; M, *A. meridianus*
Numbers 1, 3 and 4 are *meridianus* shorelines; 2, 5, 6 and 7 *aquaticus* shorelines.
In No. 3 station 0 is at the southern point and station 9 at the head of the bay.

Station	1. Brathay Rocks to Garth's Bay		2. Ash Landing to Sandy Nab		3. Wild Duck Bay (south side)		4. Town Head to Fell Foot		5. Cockshott Point		6. Pate Crag to Rose Cottage		7. Cannon Crag	
	A	M	A	M	A	M	A	M	A	M	A	M	A	M
0	0	51	38	0	0	7	2	0	130	0	2	0	60	0
1	0	6	80	0	0	0	0	1	47	0	26	0	67	0
2	2	21	95	0	0	0	0	19	103	0	42	0	136	0
3	14	1	97	0	0	1	0	9	23	0	25	0	45	0
4	59	0	9	0	0	1	1	5	84	0	50	0	15	0
5	10	0	45	0	0	16	0	0	61	0	80	0	63	0
6	190	0	0	0	0	6	0	5			38	0		
7	13	1	84	0	0	7	0	75						
8	0	23	1	0	0	4								
9	0	18	11	0	38	0								
10	0	0	21	0										
11	0	5	137	0										
12	0	10	32	0										
13	0	27	89	0										
14	1	8	75	0										
15	0	13	76	0										
16			54	1										
17			11	0										
18			49	0										

carried out in the northern zone on the west resulting in a large number of collections. As far as ordinary random collecting was concerned, attention was divided equally between the eastern and western shores.

It will be seen that in the *A. meridianus* zone at the northern end of the lake there were many blank collections, particularly on the western shores, in which *Asellus* was absent, while in the *A. aquaticus* zone in the middle part of the lake it was unusual for *Asellus* to be absent. Moreover the frequent occurrence of *A. aquaticus* at certain places on the western shores of the southern *A. meridianus* zone is in contrast to the eastern shoreline of the southern *A. meridianus* zone, where the domination of *A. meridianus* is almost complete, *A. aquaticus* never occurring in any numbers. It should also be noticed that in the northern zone of the lake the *A. aquaticus* zone on the eastern shore extends much further north than on the west.

The existence of mixed communities of the two species and the occurrence of *A. aquaticus* only at isolated stations in *A. meridianus* zones raised the obvious question whether collections made along a strip of shoreline at frequent intervals

Table 3. *Analysis of 31 dredge samples*

Dredging results	Samples	Conditions on nearest shoreline				
		aquaticus only	*meridianus* only	Mixed population	*aquaticus* dominant	*meridianus* dominant
aquaticus only	2	0	0	2	0	0
meridianus only	7	3	2	0	0	0
Mixed population	5	4	0	1	0	0
Mixed—*aquaticus* dominant	2	1	1	0	0	0
Mixed—*Meridianus* dominant	15	10	2	0	2	1

would reveal an entirely different distribution. For this reason 'crawls' were made along shorelines classified as typically *A. meridianus* or *A. aquaticus*. The results of some of these crawls are given in Table 2, two facts becoming apparent. Firstly, in a 'crawl' made on an *A. aquaticus* shoreline it was very rare indeed for any *A. meridianus* to be found; if they were present it was a case of only one or two specimens. On an *A. meridianus* shoreline the position was different, as *A. aquaticus* was liable to occur, often in some numbers, in isolated communities. Secondly, in these 'crawls' *A. aquaticus* often occurred in great numbers while *A. meridianus* tended to be much less abundant, which bore out the evidence of the shore collections generally, that the *A. meridianus* communities were usually less populous than those of *A. aquaticus*.

(*b*) *Dredge and grab collections*

The dredging results are summarized in Table 3, where only those samples with ten or more *Asellus* are included, the position indicated by this table being supported by the other dredge collections in which *Asellus* was less abundant. The

table compares the results of thirty-one dredgings with the *Asellus* population of the nearest shoreline, and should be read horizontally. For example, *A. meridianus* alone occurred in seven dredge samples at five different places. At three of these the shoreline was '*A. aquaticus*' only, while at two of them only *A. meridianus* occurred on the shore. The main point is the importance of *A. meridianus* below 2 m irrespective of whether the dredging was made off a shoreline dominated by *A. meridianus* or *A. aquaticus*. Dredgings were deliberately made off shorelines where the dominance of *A. aquaticus* had been proved by 'crawl' collections, and in every case the dredge samples were dominated by *A. meridianus*. Mixed populations occurred in which the two species were represented equally, but *A. meridianus* was in most cases the dominant species, and it was unusual indeed for a collection below 2 m to contain *A. aquaticus* only, and if so the numbers, with one exception, were small.

Table 4. *Ekman grab results off Ash Landing*

A, *Asellus aquaticus*; M, *Asellus meridianus*

Station		Depth (m) 0-0.25	0.5	1	2	3	4	5	6	7	8	9
1	A	36	2	7	7	5	0	0	0	0	0	0
	M	0	0	1	19	5*	1	0	0	0	0	0
2	A	24	46	22	5	0	0	0	1			
	M	0	0	0	38*	0	1	0	0			
3	A	106	6	2	5	3	5	0				
	M	0	1	17	36	22	4*	0				

*Limit of vegetation (*Isoetes*)

This marked feature of the distribution of the two species was examined in a little more detail by means of Ekman grab samples off the Ash Landing shore, which is completely *A. aquaticus* in character, as proved by very intensive collecting. The results of these grab collections are given in Table 4 and confirm the findings of the dredge collections as well as providing additional information on the population density. The lower limit for both species was normally about 4 m, gravid females of both species occurring at this depth. In one collection a gravid female of *A. aquaticus* was found at 5·5 m. The grab collections showed some correlation between the lower limit of *Isoetes* and the occurrence of *Asellus*. In one case the *Isoetes* did not go much below 2 m, and the numbers of *Asellus* dropped from 43 at 2 m to 4 at 3·6 m. In another series of samples *Isoetes* was present at 3·5 m and nine *Asellus* were collected, whereas at 4·5 m there was no *Isoetes* and no *Asellus* were found. The possible relationship of *Asellus* distribution to plant growth was illustrated by two grab samples at 1 m, one from bare mud and the other over *Isoetes* approximately 60 cm away. On the bare mud there was one *Asellus*, while on the *Isoetes* there were nineteen specimens. This agrees with dredge samples in which *Asellus* was absent or very few in number on bare mud, sand or gravel. The Ekman samples also show the patchy nature of the *Asellus* population.

(c) *The Islands*

These have been considered separately from the mainland shores although the character of the island shores is in no way different. The reason for separate treatment is based on the possibility that the relative isolation of the islands might provide information on the history of the two species of *Asellus* in Windermere. The position of the islands in Windermere is interesting, because they are situated in the middle portion of the lake with shorelines dominated by *A. aquaticus*. The isolation from the mainland may have given the populations of *A. meridianus* some protection from *A. aquaticus* invasion, and in the more isolated islands it

Fig. 2. The distribution of the two species of *Asellus* on the shores of the central islands of Windermere and the adjacent shores.

would take longer for *A. aquaticus* to establish itself. The occurrence of the two species on the islands is given in Fig. 2. On Rampholme, Maiden Holme and Crow Holme only *A. aquaticus* is present. Both species are present on Belle Isle, Hen Holme, Lady Holme and Thompson Holme and the Lilies of the Valley, but *A. aquaticus* is the most abundant. Rough Holme and Haws Holme, isolated and exposed, are dominated by *A. meridianus*. A further point can be made with regard to the distribution of the two species on Belle Isle. *A. meridianus* was very rare indeed on the eastern side of the island facing Bowness, whereas it was

fairly common on the western side of the island. Hartley Wife, a rock in Bowness Bay, and the Oven Bottom, a reef off Rampholme, had only *A. aquaticus*.

DISCUSSION

When the distribution of the two species is compared with the physical and chemical conditions in the lake, no correlation can be made despite the very extensive data available at the Freshwater Biological Laboratory on Windermere. There is no indication that predators or other members of the fauna are controlling the distribution. Both species of *Asellus* occur abundantly in association with the rest of the fauna, and although *Asellus* is eaten by fish there is no correlation in their distribution with fish movement within the lake. Food can hardly be a limiting factor, since both species feed on the silt, fine debris and bacteria covering the stones and leaves, a type of food the supply of which is virtually limitless.

There is, however, a correlation between the *A. aquaticus* zone of the lake and shorelines formed by the moraine material of the Troutbeck and Esthwaite glaciers. The extent of these moraines has been worked out by Cresswell (1952) and their correlation with *Asellus* distribution is shown in Fig. 1. The moraine shorelines are irregular with many bays, and contrast with the straight shores of the Bannisdale series with little, if any, covering of glacial drift to soften the austerity of the underlying rock. Moraine shores have usually been cleared for cultivation and building while the Bannisdale shores are thickly wooded. It would be natural to conclude from this that *A. aquaticus* favours the more sheltered conditions available on a moraine shore, while *A. meridianus* is adapted to the more exposed conditions of the Bannisdale shores. An examination of the Windermere collections shows that this is not the case, the distribution of both species showing no correlation with the degree of exposure of the particular habitat in which they are found.

The reason for this correlation of *A. aquaticus* with moraine shorelines is to be found outside the lake. The glacial drift of the moraine shores is easily cleared and cultivated, and it is in these areas that human habitation and activity is most abundant, first the farms and later the residences with ornamental ponds and gardens. Finally came the great development of Bowness and Windermere as tourist centres. This is in contrast to the Bannisdale shorelines which are intractable, less easily developed and therefore much less affected by human activity. The theory is put forward that *A. aquaticus* has been introduced into the lake in fairly recent times and is now in competition with *A. meridianus* which is a much older inhabitant. *A. aquaticus* could very easily have been introduced by specimens being thrown into the lake from aquaria or from the debris of ornamental ponds and fish pools, and from fishermen's live bait tins emptied at the end of a day's fishing. The available evidence for this kind of thing must be considered.

Asellus is easily transported on aquatic plants used for ornamental ponds and two examples will illustrate the point. The most intensive search in Ullswater and the surrounding district failed to find any *Asellus*, except in two artificial ponds near Glenridding, the nearest known occurrence for *Asellus* being in

Windermere ten miles away over Kirkstone Pass. One pond at Hawkhowe contained *A. aquaticus*, the other pond half a mile away at Holme Howe had *A. meridianus*. The Holme Howe pond had been stocked with water lilies from a pond in Sunderland, the Hawkhowe pond with plants from a well-known supplier of aquatic plants and aquarium material. In the case of the Hawkhowe pond the matter was tested further by ordering small samples of weed from the same dealer and collecting the associated fauna. Three *A. aquaticus* were collected, one of them a gravid female. The second example refers to the transport of *Asellus* on the roots of water lilies to a new pond at the University of Leicester. Very soon after the lilies were put into the new pond gravid *A. aquaticus* were found. *Asellus* is sold as fish food and recommended for aquaria by popular books on fish aquaria. It is also recommended in gardening journals as suitable for introduction into fish ponds, and debris from such activities thrown into the lake would contain *Asellus*. Evidence of a similar nature is given by Macan (1950) who suggests that the peculiar mollusc fauna of School Knotts Tarn, Bowness, may be the result of random introductions of this sort. It is also worth recalling that Kew (1893) quotes examples of the transport of freshwater molluscs over the country on a consignment of aquatic plants. As *A. aquaticus* is the commoner species, it is much the most likely of the two species to be transported in this way.

More indirect evidence that *Asellus* is transported by man comes from a survey of the Lake District and adjoining areas, in which 86 ponds, lakes and tarns were searched. *Asellus* was present in only 22, and of these at least 14 were artificial—either fish ponds, ornamental pools or quarry pools, at the most only one hundred years old, many being much more recent. This is in contrast to the distribution of *Asellus* in the natural lakes and tarns which are all apparently suitable habitats and have been available for 8000 years and yet contain no *Asellus*, except for Windermere, Bassenthwaite, Rydal, Grasmere and one locality in Esthwaite Water.

The close correlation of *A. aquaticus* with areas of building and land development strongly suggests introduction by debris thrown into the lake, and an old gardener on being questioned remembered throwing debris from the pond and garden into the lake, and stated that it was a frequent practice in other gardens. This theory would explain why, in the *A. meridianus* zone in the southern part of the lake, *A. aquaticus* occurs either dominant or in mixed populations on the western shore and not on the eastern. The places where these mixed populations occur in the Riddings and Wild Duck Bay areas are on moraine material from the Esthwaite glacier. The land behind has been cleared and there are farms, residences and boat-houses, and *A. aquaticus* has probably been introduced in the manner already suggested for the middle regions of the lake.

There are, however, two more serious anomalies that require explanation. Firstly, there is the complete dominance of *A. aquaticus* on the Bannisdale shores between Ash Landing and Sandy Nab, a coastline which is little developed by human activity. According to the theory just put forward, this ought to be an *A. meridianus* coastline. The reason for this anomaly is the fact that the islands

represent a series of stepping-stones linking the heavily developed area of Bowness with the opposite shore, and *A. aquaticus* has spread across and infected the shoreline. Secondly, the shoreline from Brathay Mouth round to Wray boat-house has long stretches of drift shoreline, where one would expect *A. aquaticus* and not *A. meridianus* to be dominant. Here again the answer is based on the degree of human activity. This shoreline is not heavily developed, but it is significant that of the three places on this shoreline where *A. aquaticus* is important, Brathay Bay and Wray Castle boat-house, are where visitors and boats are common.

A point which requires some comment is the dominance of *A. meridianus* below 2 m. It may be that *A. meridianus* is more a sub-littoral than a littoral form, and cannot compete with *A. aquaticus* in the littoral region. It is noticeable how when *A. aquaticus* occurs it tends to do so in large numbers to the exclusion of *A. meridianus*. It is interesting in this connection to record that in Bassenthwaite Lake only *A. meridianus* occurs, inhabiting both littoral and sub-littoral regions. Bassenthwaite is a lake with a silted and shelving shoreline, the distinction between littoral and sub-littoral being less clear cut than in Windermere. These conditions together with the absence of *A. aquaticus* may explain the patchy but abundant population of *A. meridianus* in the littoral region of Bassenthwaite Lake.

The state of affairs described for Windermere may well be unstable, and another survey of Windermere in say twenty years' time might show a different distribution of the two species. For this reason the collections, maps and general data have been deposited at the Freshwater Biological Association's Laboratory on Windermere. Finally the presence of *A. meridianus* in Windermere, Bassenthwaite Lake and other Lake District localities has implications of more general interest. Current opinion (Thienemann 1950) regards *A. aquaticus* as a northern form, while *A. meridianus* is regarded as a Mediterranean species moving northwards after the ice age. The presence of *A. meridianus* in a north-western area like the Lake District which has been recently glaciated, and the fact that *A. meridianus* is the only species found on the westerly islands of Skokholm, Bardsey, Lundy and the Isle of Man, seems to call for a reconsideration of the past history of *A. meridianus*. The evidence for *Asellus* as it stands at present has certain resemblances to the relationships of *Gammarus duebeni* and *G. pulex* described by Hynes (1954). The situation, however, is not so clear cut for *Asellus* because *A. meridianus* does occur in the eastern half of the country.

SUMMARY

1. The paper describes the distribution of *A. aquaticus* (L.) and *A. meridianus* Rac. in Windermere.

2. As far as *Asellus* is concerned the lake shores can be divided into northern, middle and southern zones. The middle zone shorelines are dominated by *aquaticus*, the southern and northern by *meridianus*.

3. No physical or chemical factor could be found that explained this distribution, but it was noticed that *aquaticus* tended to be associated with glacial drift shorelines and *meridianus* with Bannisdale slate shorelines.

4. Since there is more residential and human activity on the drift than on the Bannisdale shores, the association of *aquaticus* with drift shores may be due to its introduction by man.

5. *A. aquaticus* is regarded as a competitor to *meridianus* spreading along the shoreline from centres of human activity.

6. Below 2 m *meridianus* is the dominant form although the adjoining shore may be completely dominated by *aquaticus*.

7. The suggestion is made that *meridianus* is more sub-littoral than littoral, and unable to compete with *aquaticus* in the littoral region.

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THE COLLEMBOLA AND ACARINA OF UNCULTIVATED SOIL

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(With 1 Figure in the Text)

This paper describes part of an investigation designed to study the effects of cultivation and insecticides on the microarthropoda of soil. The habitat selected for this study was old grassland at Bellahouston Park, Glasgow, and the fauna described below was extracted from the four uncultivated plots of a 4 × 6 randomized block experiment (Fig. 1). These plots, designated 1-4, according to the block in which they were located, represent the condition of the area before the experiment was laid down. The soil was a heavy loam, derived from a considerable depth of glacial till, overlying carboniferous limestone. The herbage of plots 2,

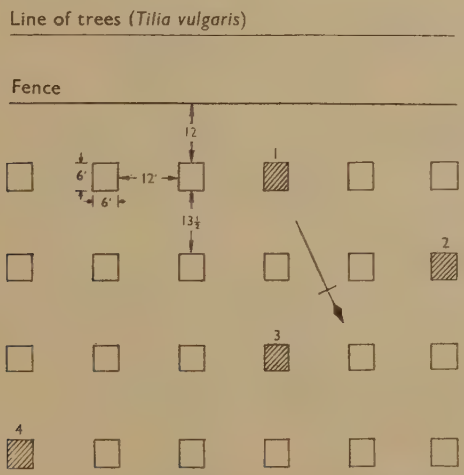

Fig. 1. The spatial relationship of the four uncultivated plots.

3 and 4 was dominated by *Agrostis vulgaris* With., *Festuca rubra* L., and *Holcus mollis* L., while in plot 1 it was thinner and dominated by *Poa pratensis* L.

Samples were taken with an implement which removed a core 2 in. in diameter. Before sampling, the herbage was cut away, and two random samples per plot were taken on 9 June, 16 October and 14 December 1951, 20 February, 18 April and 17 October 1952. In June 1951 the samples were taken to a depth of 9 in. and sub-divided to represent two strata, 0-3 and 3-9 in. in depth. On subsequent

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occasions, the samples were undivided and taken to a depth of 6 in. The animals were extracted with a flotation apparatus similar to that described by Salt & Hollick (1944), the smallest component sieve having a regular square mesh of 0·152 mm (100 mesh B.S.S.).

ANALYSIS OF DATA

The species encountered are noted in Table 1. Three species are new to science and the list includes a number of groups and species hitherto unrecorded for Britain. A detailed account of some of these forms has been published elsewhere (Sheals 1956).

Table 1. *List of species encountered*

COLLEMBOLA
Hypogastrura denticulata Bagn. Sensu Gisin 1949
Brachystomella parvula (Schaeff.)
Friesea mirablis (Tullb.)
**Onychiurus uliginatus* Gisin
**O. spinularius* Gisin
Tullbegia krausbaueri (Boern.)
T. quadrispina (Boern.)
**T. crassicuspis* Gisin
Folsomia candida Will.
F. cf. *garretti* Bagn.
F. quadrioculata (Tullb.)
Isotomodes productus (Axels.)
Isotoma viridis Bour.
Tomocerus minor (Lubb.)
Isotomurus palustris (Muell)
Entomobrya albocincta (Temp.)
Lepidocyrtus cyaneus (Tullb.)
Collembola spp. undet.

ACARINA
Cryptostigmata, Oribatei:
†*Eulohmannia ribagai* Berl.
Hypochthonius rufulus (Mich.)
Ceratozetes gracilis (Mich.)
Achipteria coleoptrata (L.)
Euzetes globulus (Nic.)
Punctoribates punctum (Koch.)
Minunthozetes semirufus (Koch.)
Oppia clavipectinata (Mich.)
Oribella lanceolata (Mich.)
O. paolii Oud.
Scutovertex sculptus Mich.
Phthiracarus anonymum Grdjn.
Cryptostigmata, Acaridiae:
Acarus siro L.
Tyrophagus castellanii (Hirst)
Rhizoglyphus echinopus (F. & R.)
Glycyphagus destructor (Schrank)
Mesostigmata:
Rhodacarus roseus Oud.
‡*Rhodacarellus epigynialis* n.sp.
Veigaia nemorensis (Koch.)
Pergamasus runciger Berl.
**P. misellus* Berl.
Macrocheles sp.
Pachylaelaps sp.
Digamasellus reticulatus n.sp.
Arctoseius cetratus (Sell.)
Arctoseiopsis minutus (Halb.)
Alliphis halleri (Canest.)
Cosmolaelaps claviger (Berl.)
**Lasioseius penicilliger* Berl.
Platyseius n.sp. Evans (in prep.)
Hypoaspis aculeifer (Canest.)
Eviphis ostrinus (Koch.)
Dinychus tetraphyllus Berl.
Olodiscus minima (Kram.)
Prostigmata:
Cheyletus eruditus (Schrank)
Heterostigmata:
Pygmephorus sp.
Acarina spp. undet.

*Species new to Britain. † In cultivated soil only; represents family new to Britain. ‡Genus new to Britain.

The composition of the population over the five sampling occasions during the year October 1951-52 is shown in Table 2. The June samples have not been included in this assessment, for being deeper they were not strictly comparable. In the case of Oribatei and Mesostigmata, the species counts refer to adults only, for owing to taxonomic difficulties the immature instars of these groups were

assessed separately. The population was dominated by the Acarina, which accounted for 58% of the Arthropoda. The most numerous mites were the Oribatei, the dominant species being *Minunthozetes semirufus*. Also prominent were the Mesostigmata and particularly the delicate Rhodacaridae, represented here by two species the more numerous being *Rhodacarellus epigynialis*. The Collembola made up 39% of the arthropod collection and were dominated by *Tullbergia krausbaueri*.

Table 2. *The percentage composition of the arthropodan community in the upper 6 in. of soil over five occasions between October 1951-52*

Total number of Arthropoda collected = 4710

	% of Arthropoda
Collembola	39·4
Acarina	57·7
Other Arthropoda	2·9

ACARINA	% of Acarina
Oribatei	57·1
Acaridiae	15·7
Mesostigmata	26·0
'Trombidiformes'	1·1

COLLEMBOLA	% of Collembola
Euedaphic forms:—	
Onychiurus uliginatus	12·8
O. spinularius	4·8
Onychiurus spp. undet.	1·8
Tullbergia krausbaueri	25·4
T. crassicuspis	3·1
Folsomia candida	13·7
Isotomodes productus	13·5
Hemiedaphic forms:—	
Brachystomella parvula	5·6
Hypogastrura denticulata	5·4
Friesea mirabilis	7·1
Folsomia quadrioculata	1·8
Unidentified and other Collembola	4·8

ACARIDIAE	% of Acaridiae
Acarus siro	14·7
Tyrophagus castellanii	9·3
Rhizoglyphus echinopus	42·3
Glycyphagus destructor	33·6

ORIBATEI	% of Oribatei
Ceratozetes gracilis	1·7
Achipteria coleoptrata	4·2
Euzetes globulus	1·0
Punctoribates punctum	24·0
Minunthozetes semirufus	42·6
Oppia clavipectinata	5·6
Oribella lanceolata	4·7
O. paolii	5·7
Scutovertex sculptus	1·3
Unidentified and other Oribatei	0·4
Immature Oribatei	8·7

MESOSTIGMATA	% of Mesostigmata
Rhodacarus roseus	22·3
Rhodacarellus epigynialis	26·6
Veigaia nemorensis	[3·7
Pergamasus runciger	10·2
P. misellus	3·1
Digamasellus reticulatus	3·2
Arctoseius cetratus	1·0
Arctoseiopsis minutus	1·3
Cosmolaelaps claviger	0·4
Lasioseius penicilliger	0·8
Platyseius sp.	1·0
Hypoaspis aculeifer	0·7
Eviphis ostrinus	2·1
Olodiscus minima	4·2
Unidentified and other Mesostigmata	2·5
Immature Mesostigmata	16·6

The populations of the two strata in June 1951 have been compared on a volume basis. Thus, as the population of the lower stratum (3-9 in.) represented double the volume of soil occupied by the upper population, the lower populations were halved. A comparison of the densities in the two strata is given in Table 3. It will be noted that in most cases the population density in the upper stratum was significantly greater than that in the lower soil. In no case did the reverse obtain.

although in *Onychiurus* spp. and in the *Rhodacaridae* the animals were particularly abundant in the lower soil.

The horizontal dispersion of the animals was also examined statistically, and the results can be summarized by noting that of the groups and species analysed (listed in Table 4), only in the analysis of the hemiedaphic Collembola and Acaridiae was the inter-plot variation less than that occurring between samples within each plot. Moreover, in most cases the values of F for plot differences were highly significant, indicating that the fauna was not distributed at random, and that even within this small area marked and consistent differences in the quantitative composition of the community obtained. The more outstanding differences were apparent when plots 1 and 3 were compared with each other and with the other two plots. Plot 1 was characterized by a high population of *Onychiurus* spp.,

Table 3. *Vertical distribution of Arthropoda, June 1951*

	Relative density in 3-9 in. stratum (density in 0-3 in. stratum = 100·0)	F†
Collembola	39·0	14·05*
Tullberginae	43·9	45·83**
Tullbergia krausbaueri	24·5	15·52*
Onychiurus spp.	122·7	–
Hemiedaphic Collembola	4·9	37·10**
Acarina	12·7	10·68*
Oribatei	7·2	20·34*
Minunthozetes semirufus	9·3	13·91*
Punctoribates punctum	3·9	23·16*
Immature Oribatei	0	–
Rhizoglyphus echinopus	10·3	1·82
Mesostigmata	37·2	3·95
Rhodacaridae	100·0	–
Rhodacarellus epigynialis	157·1	1·41
Immature Mesostigmata	6·9	22·00*

† Obtained in analyses of square root transformed data. Degrees of freedom: $n_1 = 1$, $n_2 = 3$. Levels of significance indicated thus: $*P=0{\cdot}05$, $**P=0{\cdot}01$.

and by a low Oribatid population, while in plot 3 the populations of *Folsomia candida* and *Isotomodes productus* were significantly greater than those in the other three plots.

For the purposes of work to be described elsewhere it was desirable to make observations at times when the population was expected to be high, and for this reason no samples were taken between April and October 1952. The data recorded in Table 4, however, are sufficient to indicate the general seasonal trend of the population at Glasgow. In no case were there significant differences between the populations of October 1952 and those of October 1951, and on the whole the seasonal fluctuation was most marked in Collembola. The April population of Collembola was significantly lower than that of any other sampling occasion, although in the analyses of the constituent groups and species significant differences

were less frequent. In *Onychiurus* spp., although the observed fluctuation was considerable, in no comparison were the differences significant.

The only acarine group showing a definite seasonal trend was the Oribatei. The lowest adult populations of these mites occurred in December, and the highest in February and October. In *Punctoribates punctum*, the December population was significantly lower than both those of October 1951 and February 1952.

DISCUSSION

(*a*) *The density and composition of the population*

In the present study the average arthropodan population of the upper 6 in. of soil over the five sampling occasions during the year October 1951-52 was 5·81 individuals per cm^2. Of these 2·28 were Collembola and 3·35 Acarina. Owing to differences in time and depth of sampling and to the variety of extraction methods

Table 4. *Seasonal fluctuation of Arthropoda*

Seasonal totals of square root transformed data, original data in parentheses

	Oct. 51	Dec. 51	Feb. 52	Apr. 52	Oct. 52	S.E.*
COLLEMBOLA	54·8 (407)	58·7 (449)	50·2 (340)	33·7 (150)	61·0 (508)	5·0
Tullbergia krausbaueri	31·4 (132)	20·7 (64)	20·2 (69)	13·2 (35)	33·1 (171)	5·7
Onychiurus spp.	21·9 (83)	22·9 (94)	17·7 (58)	9·2 (30)	22·1 (94)	4·9
Folsomia candida	18·7 (69)	21·4 (98)	11·5 (40)	6·7 (23)	11·4 (25)	3·4
Isotomodes productus	13·7 (42)	20·8 (61)	21·3 (65)	6·7 (12)	17·4 (71)	3·3
Hemiedaphic Collembola	21·6 (63)	28·8 (106)	24·0 (82)	13·0 (34)	27·9 (108)	3·0
ACARINA	65·8 (567)	51·6 (373)	60·4 (588)	50·1 (362)	74·4 (827)	6·5
Oribatei	47·4 (331)	31·3 (178)	46·7 (405)	40·9 (274)	49·7 (364)	5·7
Punctoribates punctum	27·8 (122)	10·1 (21)	22·5 (120)	19·1 (64)	16·6 (45)	3·7
Minunthozetes semirufus	25·7 (100)	20·0 (85)	28·2 (161)	28·2 (131)	35·4 (185)	4·1
Oribella spp.	15·2 (37)	6·7 (15)	9·6 (27)	9·9 (21)	19·0 (61)	2·1
Immature Oribatei	15·4 (42)	10·5 (28)	11·0 (31)	5·6 (12)	10·2 (22)	2·4
Acaridiae	19·1 (60)	17·4 (54)	10·5 (38)	6·4 (9)	34·7 (267)	6·2
Mesostigmata	35·1 (159)	32·4 (137)	31·7 (142)	24·1 (76)	35·4 (193)	3·7
Rhodacaridae	26·0 (87)	19·9 (68)	22·1 (69)	15·3 (37)	21·0 (85)	4·1
Rhodacarellus epigynialis	14·5 (34)	14·3 (38)	20·1 (60)	14·1 (31)	9·5 (25)	3·2
Immature Mesostigmata	14·3 (30)	9·4 (13)	12·0 (21)	9·0 (14)	15·2 (39)	2·5

* 12 degrees of freedom. Values, $\sqrt{2}\,t$:—*P* 0·05, 3·08; *P* 0·01, 4·32; *P* 0·001, 6·11.

which have been used, it is difficult to make useful comparisons with the results of other workers. Thus, during the course of the present study it was found difficult to extract animals from the soil under examination by heat-desiccation methods, and this was particularly so in relation to the small mesostigmatic mites. This may have been due largely to the heavy nature of the soil studied, for on drying the material set into a hard mass and probably imprisoned the animals.

Salt *et al.* (1948) used a flotation apparatus to assess the microarthropod population of a Cambridge pasture. Their smallest sieve was one of bolting silk (0·1 mm square mesh), and they recorded in November 1943 4·31 Collembola and 11·98 Acarina per cm^2 for the upper 6 in. of this soil. When compared with this result, the average Glasgow population is low, but if the highest seasonal population of

Collembola in the Glasgow soil is used for comparison (3·1 per cm^2, October 1952), the difference is less marked. In the case of Acarina the discrepancy is much greater. A factor which has to be considered, however, is the collection by flotation methods of the remains of dead mites, particularly Oribatei. Salt *et al.* did not determine their Acarina in detail and do not mention this contingency, but had these remains been included in the Glasgow assessment, the numbers of adult Oribatei would have been very much greater.

In the majority of recent studies, heat-desiccation methods of extraction have been used. These techniques are eminently suitable for organic soils where flotation methods are virtually useless, but being dependent upon the reactions of forms of great physiological diversity to the stimuli applied, a bias towards groups reacting favourably must be expected. It should be noted, however, that flotation methods may also give a biased result, for it is suspected that an unduly low estimate of trombidiform mites is given by this technique. These mites were encountered in very small numbers at Glasgow (0·03 per cm^2), and Evans (1951) considered that a large proportion of these delicate forms were destroyed during the initial washing process. Using a heat-desiccation technique Macfadyen (1952) recorded an average of 12·07 Oribatei per cm^2 in the upper 5 cm of soil for the *Molinia* areas in the Cothill fen. This is greatly in excess of the 1·91 oribatid individuals per cm^2 of the Glasgow soil, and there can be little doubt that the difference here is due largely to environmental factors. The mesostigmatic population at Glasgow (0·87 per cm^2) was greater than those recorded by Macfadyen, although here depth of sampling may be influential, for the Rhodacaridae, which dominated this community at Glasgow, were also seen to be particularly abundant in the lower soil. Weis-Fogh (1948) used the Berlese apparatus for a study of the mineral soil of a grass plain in Jutland. His populations of Collembola and Mesostigmata were low, but the oribatid population was only slightly lower than that at Glasgow, while the numbers of trombidiform mites collected were much greater than in the present study. Macfadyen has commented on Weis-Fogh's results, observing that, whilst the extremes of climatic conditions to which the habitat was subjected could have been responsible for the low population, it was also possible that the sampling methods adopted, and the use of the water jacket apparatus, could have led to a low assessment. In so far as oribatids are concerned, the results of the present study suggest that Weis-Fogh's low population was due to environmental factors; and whilst his low assessment of Collembola and Mesostigmata may have been due in part to the extraction technique used, it must be noted that his samples were only 5 cm deep, and both these groups include forms which are known to inhabit the deeper layers of mineral soils.

A circumstance which requires further consideration is the low population of immature Oribatei and Mesostigmata in the Glasgow soil. Whilst this could have been due to a loss of small instars during extraction, this explanation is not entirely adequate, for a similar loss was not evident in Collembola and Acaridiae. Although detailed counts were not made, it was quite obvious that in the collections of these two groups immature forms were at least as numerous as adults.

A similar deficiency of immature Oribatei was noted by Riha (1951) in a study of calcareous soils in woodland near Vienna. Here further observation indicated that the immature forms of a number of the species encountered lived in other habitats, for they were found in dead wood, under bark and in litter. Apart from *Hypochthonius rufulus*, the species encountered by Riha were not found at Glasgow. Nevertheless, most of the species occurring in this soil have also been collected from other habitats, e.g. moss, litter, and from lichens and moss on trees (Michael 1884-88, and Van der Hammen 1952). It is also particularly interesting to note that Michael found the nymphs of *Minunthozetes semirufus* burrowing in the stems of grasses. In view of this indirect evidence, it is not unreasonable to suppose that the deficiency of immature Oribatei in the soil studied might also have been due in part to a preference of these forms for other habitats. The deficiency of immature Mesostigmata, whilst not so marked, is sufficient to indicate the possibility of a similar phenomenon.

(*b*) *Vertical distribution*

Many workers have noted the uneven vertical distribution of the fauna in uncultivated mineral soils, and in view of the surface concentration of organic debris which obtains in such soils, it is hardly surprising to find a similar concentration of saprophagous and mycetophagous species, together with populations of their predators. With the exception of *Tullbergia krausbaueri*, the results for Collembola agree with the findings of other workers. The marked and highly significant difference between the densities of those species noted by Gisin (1943) as being hemiedaphic, lends further support for this morpho-ecological classification. With regard to *Onychiurus* spp., Glasgow (1939) found *O. ambulans* to be amongst the inhabitants of the deeper soil, and Strenzke (1949) noted *O. armatus* as a deep living species. In the case of *Tullbergia krausbaueri*, the density of which was significantly greater in the upper layer, the Glasgow results are not in complete accordance with those of other workers. This species has been noted as a denizen of the lower soil (e.g. Frenzel 1936, Schaller 1949, and Strenzke 1949) and in Macfadyen's study (1952), it was more abundant in the 5-10 cm layer than in the 0-5 cm stratum. However, the comparatively broad strata examined in the present study may have obscured the true vertical distribution of this species.

The surface concentration was very pronounced in the case of Oribatei, and Macfadyen (1952) also noted that, in general, Oribatei were less deeply distributed than Collembola, while Strenzke (1952) considered these mites to be predominantly hemiedaphic in character. In the analyses of Mesostigmata, no significant differences were obtained between the densities of the Rhodacaridae in the two layers; and, in the case of *Rhodacarellus epigynialis*, the density of the lower population was non-significantly greater. This group of mites has been observed by Frenzel (1936) and Willman (1935) to be amongst the few denizens of the lower soil. The writer has also noted a deep distribution for this family in arable soil at Auchincruive, Ayrshire, and in upland pasture soil at Lephinmore, Argyll.

(*c*) *Horizontal distribution*

The non-random distribution of natural populations is well known. Such dispersions have been found to obtain in plant communities, particularly in grassland (Blackman 1935); and of several examples in animal communities, Salt & Hollick (1946) demonstrated a non-random horizontal distribution of elaterid larvae, mainly *Agriotes sputator* (L.) in pasture. In the present study the high values of F obtained in the analysis of many of the plot differences indicate that these differences were consistent from one occasion to another. The present investigation was not primarily designed to study the effect of comparatively small environmental differences, consequently the precise nature of the factors influencing this distribution cannot be established, although some suggestions can be made. The prominence of the xerophytic collembolan, *Isotomodes productus* in plot 3, and the abundance in plot 1 of *Onychiurus* species, suggests an orientation in relation to moisture conditions (vide Gisin 1943, 1952) with the implication of moist conditions in plot 1. However, evidence directly opposite in character is revealed by the distribution of *Minunthozetes semirufus*, which Strenzke (1952) noted to have a preference for wet soils, although he also observed this species to be tolerant of a wide range of conditions. Chemical analyses of the plots revealed no major differences, but there were considerable differences in the vegetation, for in plot 1 the turf was not so thick and *Poa pratensis* was much more abundant here than in the other 3 plots. Thus there may have been a direct or indirect relationship between the hypogeal fauna and the composition of the sward. In fact the very thinness of the turf in plot 1 might well have been responsible for the lower poulation of the predominantly hemiedaphic Oribatei.

(*d*) *Seasonal fluctuations*

The seasonal differences were, on the whole, most marked in the Collembola. These insects were most abundant in October and December, and least numerous in April. Moreover the June samples, although not strictly comparable, nevertheless indicated a low summer population. This type of fluctuation appears to be common in British mineral soils, and the evidence of a number of investigators (e.g. Glasgow 1939) suggests that the seasonal abundance of these insects is determined largely by changing climatic conditions influencing the temperature and humidity of their environment.

The highest populations of adult Oribatei occurred in October and February, and the lowest in December. The December drop was most marked in *Punctoribates punctum*, for the December population of this species was significantly lower than both those of October 1951 and February 1952. It was also quite evident in the analysis of *Oribella* species, although the increase to February was not significant. This December drop could hardly be attributed to adverse climatic conditions, for the collembolan population was at a high level during this month. Moreover meteorological data recorded at Renfrew (about 2 miles distant in the same valley) showed that falling temperatures could not be responsible, for lower

temperatures obtained during January and February, and although excessive moisture might be considered a possible cause, this is also unlikely for most of the species concerned were noted by Strenzke (1952) to prefer damp or even wet conditions. It must also be noted that the Oribatids have a particularly lengthy life cycle. Michael (1884-88) observed that many species required a year or more to complete their development. Cleat (1952), who reared 125 individuals of *Scheloribates laevigatus* Koch, noted that the shortest duration of pre-adult life was 45 days, and the longest 115 days, the animals being kept in a saturated atmosphere at 25° C. In cultures designed to simulate natural conditions, Rooseboom (quoted by Van der Drift 1951) also observed a slow development and noted that in most cases the duration of the third nymphal instar of *Nothrus sylvestris* Nic. was at least 2-3 months. Hence it is unlikely that the increase between December and February was due to reproduction, and consequently movements of mites during this period are indicated. Rayski (1945) encountered little seasonal variation in oribatid populations in eastern Scotland, but his samples also embraced the surface herbage. Again, this December drop was not apparent in Macfadyen's habitats. Riha (1951), however, encountered marked seasonal changes, and she considered that two of the minima were related to the propagation rhythm of the animals and occasioned by a migration of adults to other habitats for copulation and egg-laying. Hence in relation to Oribatei a certain similarity exists between the results of the present study and those of Riha's investigation, the low immature : adult ratio, and the occurrence of minima, apparently not directly related to climatic conditions, being common to both localities.

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SUMMARY

1. The quantitative composition of the Collembolan and Acarine community of uncultivated land at Glasgow is described, and the nature of the vertical, horizontal and seasonal distribution of the major groups and species examined statistically.

2. In most cases the population density of the 0-3 in. layer of soil was significantly greater than that in the 3-9 in. stratum. The Rhodacaridae (Acarina), and *Onychiurus* spp. (Collembola), however, were particularly abundant in the lower stratum.

3. The animals were not distributed horizontally at random, for significant differences were noted between the populations of four plots within the area.

4. The seasonal fluctuation of Collembola could be attributed directly to climatic conditions but the phenology of Oribatei could not be explained in this way. It is concluded that the seasonal fluctuation of Oribatei was due in part to movements by the mites, and evidence is cited to suggest that these may have been associated with the reproductive cycle of the animals.

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SOME ECOLOGICAL RELATIONSHIPS OF NATURAL POPULATIONS OF CALLIPHORINE BLOWFLIES

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(With Plates 4 and 5 and 1 Figure in the Text)

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INTRODUCTION

The carrion-feeding Calliphorinae form a distinct ecological group which utilizes mammalian and avian tissues for rearing its young. Infestation of the dead carcase is the classic niche of the group; cutaneous myiasis of the living body, as a major food niche in the community, is almost certainly a recent reaction to man's influence. The adult blowfly can live on plant carbohydrate, but the female requires protein for maturation of ovaries. This is, however, provided by the carrion sources of larval food. Thus, within a major community, and assuming that macroclimatic limits are not transgressed, the limiting requirements of blowflies should be twofold. They require a suitable subterranean or floor stratum for the larvae for pupation and development, and shelter and carbohydrate sources for the adult. They should also require the ecological conditions necessary for persistence of an adequate carrion population in the floor stratum, i.e. suitable habitat conditions for maintenance of small-mammal and/or bird fauna, and edaphic conditions which allow the carcases to remain integrated in the biocoenose. This latter means, among other things, that they must not desiccate over-rapidly, e.g. in excessively arid ecoclimates, must not be removed out of the biocoenose, literally, as by intruder scavengers, or in effect, by being inaccessible to the adult fly, e.g. in subterranean recesses or under water. Nor must they be so distributed that larvae, though able to feed on them, will subsequently perish, e.g. on bare rock, beaches, dry sand or marsh.

This simple picture is, however, complicated by the increasingly important alternative food niche, myiasis. This myiasis association appears to involve two, and possibly three, adjacent food meshes, the evolutionary relationships of which are not clear. Certain larvae feed on necrotic tissue on the living animal such as foot-rot lesions (*Fusiformis nodosus* infection) of sheep. This is probably a simple variant of the carrion feeding niche; the diseased tissue is a carcase, though incomplete, which happens to be carried on the living animal. This 'scavenging myiasis' is essentially beneficial; a modern variation is the use of surgical maggots for cleaning up deep-seated ulcers which are inaccessible to the surgeon's knife. Certain blowfly species will oviposit in fresh wounds in living tissues. The earliest decomposition odours from a killed tissue, e.g. from newly spilled blood, are presumably different from those originating from more obviously putrefactive changes, and though little is yet known of the essential attractions to which blowflies respond, it may be argued that such 'wound myiasis' and the scavenging myiasis arise from separate stimulants for the fly. Certain species will oviposit on the wool or unbroken skin of living sheep. Such myiasis is frequently of obviously putrefactive origin—urine staining of the perinaeal region, bacterial activity in dead surface tissue, i.e. decaying wool, skin detritus or sebaceous secretion; on the other hand many instances of myiasis do not seem to be related to any obvious source of decomposition odours, oviposition having occurred on apparently normal wool or skin. Thus, cutaneous myiasis of sheep, though usually regarded as an extension of the carrion feeding food link via the more primitive scavenging myiasis habit, may be a development from the wound myiasis link; it may even have arisen independently. Whatever their evolutionary origins, the relevant point is that two myiasis associations, cutaneous myiasis of sheep, and to a lesser extent wound myiasis of domesticated animals on the range, may have an important bearing on the community inter-relationships outlined above. Thus in a community dominantly influenced by a sheep husbandry system blowfly myiasis could obviously alter very considerably the basic blowfly-small mammal-vegetation complex. Sheep under management may be largely independent of their primitive community relationships. If they form an important fly population source for those species forming a 'myiasis link', then the earlier stated second limiting requirement, a habitat for a natural mammalian fauna, becomes less important, and the simple concept of a blowfly-carrion-habitat biocoenose requires to be revised.

The ecological repercussions of this food web are of obvious importance. The myiasis aspect, under modern sheep husbandry conditions, has long claimed attention in Britain, Australia and South Africa, and much effort has been expended on perfecting preventive and control measures. Similarly with wound myiasis, the growing importance of the problem, particularly in the United States, has led to attention being given to its more specifically myiasis aspects. Associated with these applied studies there has been a long series of notable contributions on the ecology of myiasis in sheep and cattle.

The fundamental community relationships of the blowfly group on the other

hand have until recently remained largely unexplored, though some sporadic efforts have been made to unravel the ecological skein, e.g. those of Graham Smith (1916), Wardle (1927), Fuller (1934), Bruce & Knipling (1936), Evans (1936), Deonier (1940), Ullyett (1950). Recent American work on fly populations (Lindquist, Yates & Hoffman 1951, Quarterman, Mathis & Kilpatrick 1954) suggests a quickening of interest in the broad ecology of blowfly populations in general, an interest reflected in this country in Green's work on control (1951 et seq.).

The present paper describes observations made over a number of years on the blowfly population of Crosby aerodrome, near Carlisle, and of some nearby areas. A general account is given of the relation of year and season to the composition of the population, and its local distribution is examined in relation to the vegetation structure. It is intended to deal with other facets of the community and physical relationships of the group in later papers.

CENSUS METHODOLOGY

For the enumerative aspects of this work existing sampling methods were inadequate, and much work has been done in improving and checking techniques. The work will be described in detail in separate papers, and only brief descriptions of the methods used are given here. The results are compiled from three main sources of information.

(*a*) *Bait-trapping*

Three methods of bait-trapping have been used: serial trapping in which single traps in fixed positions sampled an area over a period of years; short term trapping in which traps distributed in low density over the areas being examined were kept going for several days, the traps being emptied and the bait renewed periodically; and massive trapping in which large numbers of traps were used for a single trapping. Two or three hundred traps might be used distributed over limited areas with a trap spacing of usually 10 yd, but on occasion as low as 5 yd.

For trapping work we make use of two recognizable units of area, the location and the subsection block, and a third unit, the section. This last is the working unit of area. It is not an ecological entity, but represents any particular piece of territory which by reason of position, ease of access, or nature of land use can conveniently be treated as a working unit. It is usually less than a quarter-mile square, but may be of any degree of ecological heterogeneity from a uniform field to a highly complex mosaic of either or both vegetational and physiographic facets. A section may consist of only one or of several 'subsection blocks'. These latter are ecological units, and have already been described in relation to trap-catch variability (MacLeod & Donnelly 1956). They are restricted to uniform vegetational or physiographic facets of the section and correspond to major fragments of the mosaic complex of Du Reitz (Carpenter 1938). The location, a physically uniform association fragment, is rarely more than a few yards in diameter, and has been little used in bait-trapping, except in experiments on

the range of variability of trap catches. It has been used principally in our tent-trapping work.

For comparing the mean catch from groups of traps sampling sections or subsections, we have shown (1956) that the variance is more reliably estimated from a simplified expression of the relationship of standard deviation to mean than from the information supplied by the sample itself. The equations are:

Sections	S.D. = mean+1, for means up to 12.
	= 0·5 mean+7, for means over 12.
Subsections	S.D. = 0·8 mean+1, for means up to 20.
	= 0·4 mean+9, for means over 20.

Bait-trap estimates of relative proportions of the component species of a population are of course subject to wide error because of possible differences in response between species and between sexes. Where the conclusions refer only to the population at risk of capture by the traps, the results are nevertheless of comparative value, and indeed the field investigator must rely on bait-trapping results for the great bulk of his information. For quantitative work on the actual populations of blowflies, however, the relation of these bait-trap estimates of relative numbers to their true ranking must be assessed, and we have attempted to do this by two independent methods.

(*b*) *Tent-trapping*

The principle of this method is that at night when the flies are resting, as much as possible of the area being examined is covered by tents. The tents, each enclosing one square metre, are topped by gauze cones terminating in traps. In the morning any flies resting overnight on the enclosed metre make for the patch of light represented by the cone, and are trapped. Ideally the whole of an area, say an acre, would be covered, and a single catch would give not an estimate but the actual parameters of the adult population at rest overnight. In practice only a small proportion of an acre, up to 100 m^2, has been tent-trapped at any one time, but it is clear that by increasing the number of tents the estimate can be made to approximate more and more closely to the true value, so that the method yields an unbiased estimate. To obtain this the tents require to be distributed either randomly or on each significant ecological element of the area in proportion to its relative size. So far our work has not satisfied these requirements, and unbiased estimates are not yet available by this method.

Assuming a density in the order of 500 flies per acre, only one fly on the average would be expected per ten tents per night. Flies may take two or three days to enter the trap in unfavourable weather conditions, and in practice the tents are usually left *in situ* for two days. The method is thus severely limited for general application, but provides a useful accessory tool for population sampling.

(*c*) *Release-recapture estimates*

The capture-recapture or Lincoln-index method for estimating density of

population by use of marked individuals has serious limitations in so far as the blowfly group is concerned. A detailed examination of the application and limitations of the method for blowfly work will be published separately, but we may briefly refer here to one major source of difficulty, emigration, because of its bearing on the work to be described.

Ideally, the method is designed for closed populations, and under such conditions it is necessary only to adjust for dilution by birth and death. In populations able to emigrate out of the area, however, a source of bias is introduced which at present cannot be covered by numerical adjustment. Assuming that blowflies are nomadic, the random movements of a group of marked flies will inevitably result in an outward spread with decreasing density. Since at the limit of the distribution pattern there is no random inward movement of marked flies, the level of the distribution curve within any arbitrarily chosen limits will decrease, even though the general shape remains stable. This 'emigration rate' may well vary according to the habitat conditions at the release point. Thus if the area under test forms a local focus of high concentration, it is probable that this is related to the suitability of some environmental factor or factors relative to the adjacent areas, where the population is lower. These same factors should 'bind' the marked flies also, to the extent that the rate of outward spread is reduced. At the opposite extreme the release area might be surrounded by areas with a higher level of population, indicating a greater environmental suitability. In such case emigration might be expected to be excessively rapid. An experimentally determined value for emigration rate may thus not have general application, and reliable estimates of population based on recovery of marked flies will require accurate foreknowledge of the emigration rate to be expected for each habitat being tested in relation to its neighbouring habitats. Otherwise in for example the comparison of two areas, if their emigration rates differed, one would have a more inflated estimate of population than the other. Further, before the estimated population can be related to area, the limits of the habitat being tested must be known, i.e. the range of territory beyond the traps from which flies are being drawn by the attraction of the bait.

In the present paper some provisional estimates of population densities are made from recovery data. These are based on the following assumptions, the second empirical, but the other three supported in part at least by experimental evidence:

(1) The mortality rate of wild flies is in the order of 2% per day in summer and 4% in autumn.

(2) The normal range of simple undirected, i.e. questing, flight is from 50 to 100 yd, i.e. the unit of fly territory is an area of not more than 200 yd diameter. This is an arbitrary unit required for the study of dispersal rate and is not to be confused with the ecological units of area previously defined, the location and subsection block. It could be described as the area within which 50% of a concentration will still remain after two successive bursts of random flight, assuming the average straight-line distance covered in a flight to be 75 yd.

(3) The zone of influence of traps distributed over a unit of territory extends half way into adjoining units.

(4) Released flies disperse by nomadic movement so that within 2 days the released population is distributed over an area of at least 1 mile radius, with a density decreasing from the centre in inverse proportion to a distance function whose value lies between twice the distance and the square of the distance, in territory units.

On the basis of the density varying with the square of the distance, the mean proportion of marked flies which remains within the range of attraction of traps distributed over the 'release unit' of territory during the first week has been taken as approximately 16% of the releases (MacLeod, in preparation).

Table 1. *Annual totals from serial trapping in 5-day periods at Crosby*

In this and the following tables *L.c.* = *Lucilia caesar*, *L.ill.* = *L. illustris*, *L.amp.* = *L. ampullacea*, *L.s.* = *L. sericata*, *L.silv.* = *L. silvarum*, *C.e.* = *Calliphora erythrocephala*, *C.v.* = *C. vomitoria*, *P.t-n.* = *Phormia terrae-novae*, *Cyn.* = *Cynomyia mortuorum*.

	Effective Periods	Total	Percentage of Total								
			L.c.	*L.ill.*	*L.amp*	*L.s.*	*L.silv.*	*C.e.*	*C.v.*	*P.t-n.* (actual)	*Cyn.*
1949	7	11 028	3·7	8·1	0·53	0·66	0·63	80	6·3	(14)	0·51
1950	9	5 221	22	23·6	1·24	0·45	1·28	40	1·16	(2)	0·7
1950 (excl. 5-9 June)		2 898	13	9·6	1·9	0·1	1·9	71	1·1	0	1·1
1951	7	5 754	2·1	2·1	0·19	0·05	0·31	91	4	0	0·1
1952	7	4 456	5	13	1·2	0	0·16	77	2·7	0	0·23
		26 457									

YEAR AND SEASON DIFFERENCES IN SPECIES COMPOSITION

Between 1949 and 1953 a serial trapping experiment was run intermittently on a disused aerodrome on Crosby Moor, which is a mixed farming area at about 150 ft altitude immediately south of the old Roman wall, north of Carlisle. Five spherical traps were used, each situated in a different vegetational environment. Trappings were made at intervals of 2 to 5 weeks; each trapping period lasted 5 days, the bait (rabbit flesh) being renewed daily. The same five trap-sites were used throughout.

(*a*) *Annual differences*

The annual totals, and the percentage of the total represented by each species, are given in Table 1. These annual total catches are, of course, subject to the accident of weather conditions during the trapping periods, and differences are to be expected; there is no evidence of a secular trend in the total population.

In 1950 one catch, that in early June, was quite exceptional, *Calliphora erythrocephala* Mg. being outnumbered by both *Lucilia caesar* L. and *L. illustris* Mg.

Table 2. *Serial trapping results in relation to season*

The percentage of the catch formed by each species (both sexes together) is shown in parentheses

	Total	*L.e.* ♂	*L.e.* ♀	*L.ill.* ♂	*L.ill.* ♀	*L.amp.* ♂	*L.amp.* ♀	*L.s.* ♂	*L.s.* ♀	*L.xiliv.* ♂	*L.xiliv.* ♀	*C.e.* ♂	*C.e.* ♀	*C.v.* ♂	*C.v.* ♀	*P.l-n.* ♂	*P.l-n.* ♀	*Cyn.* ♂	*Cyn.* ♀	Unident. *Lacrtia.*
May to mid June	9 804	192 (1·96)	706	171 (1·75)	1 251	26 (0·26)	20	2 (0·02)	25	10 (0·1)	13	816 (8·32)	6 229	20 (0·2)	150	1	1	9 (0·09)	42	21 (0·2)
Mid June to end July	3 041	68 (2·24)	443	55 (1·81)	465	2 (0·07)	07	1 (0·03)	15	7 (0·23)	48	308 (10·13)	1 969	26 (0·85)	74			5 (0·16)	13	37 (1·22)
Aug. to mid Sept	1 408	31 (2·2)	243	01 (1·5)	046	1 (0·07)	26	1 (0·07)	36	1 (0·07)	09	415 (29·5)	2 468	28 (1·99)	123	10 (0·71)	3	4 (0·28)	12	217 (15·4)
Mid Sept to mid-Oct.	7 567	5 (0·07)	119	1 (0·01)	90	(0·14)	11	1 (0·01)	13	1 (0·01)	3	376 (4·97)	5 813	27 (0·36)	619					
	Overall %	7		10.		0·65		0·35		0·55		77		4		0·05		0·5		

This occurred in no other trapping period. Even when this catch is excluded, however, the composition over the year shows an exceptional number of *Lucilia* spp. Except for this year, *L. caesar*, *L. illustris* and *Calliphora vomitoria* L. showed unimportant variations from year to year. The numbers of *Lucilia ampullacea* Villen. and *L. silvarum* Mg. were too low for differences to be reliable. *L. sericata*, present throughout the 1949 fly season, was also present in numbers in May-June of 1950 but rare subsequently, and disappeared from the catches by 1952. *Phormia terrae-novae* R.-D., also present in 1949, disappeared during 1950. Although both species were taken in other experiments in subsequent years, their decline and disappearance in the serial trap samplings are suggestive of secular change in their numbers.

(*b*) *Seasonal differences*

The catches for 1949 to 1952, and for the early part of 1953, have been grouped according to season in Table 2. A limited number of *Lucilia* spp., rendered unidentifiable through damage by beetles and spiders when in the traps, are entered in the last column. The following points are noteworthy.

(1) The blowfly population in this area consists of at least twelve species. (*Acrophaga subalpina* Ringd. was taken in April. Two other species, *Lucilia richardsi* Collin and *Calliphora loewi* Enderlein, occurred in other experimental trappings, though not in the serial trapping.) Assuming for the present that the numbers of each species responding to the bait are in proportion to their relative numbers in the population, one species, *C. erythrocephala*, predominates at all seasons; it is practically the only species represented in the early and end-of-season catches, but during the summer *Lucilia illustris* and *L. caesar* form a considerable part of the population. The other species are all relatively rare, though *Calliphora vomitoria* appears in some numbers in the late season. The existence of this seasonal difference in blowfly species pattern as a source of variability in population studies has already been demonstrated (MacLeod 1956). The results were examined for differences between years in relative proportions for each season. The three major groups show irregular variation, with no suggestion of a trend.

(2) The sheep-myiasis species, *Lucilia sericata*, at no time exceeded 1% of the total population and formed only 1 to 4% of the *Lucilia* group.

(3) Of the two other potential myiasis producers, *L. caesar* and *L. illustris*, the latter tends to be more numerous, the preponderance being more pronounced in the warm August to mid-September period (cf. also Cragg & Thurston 1950, for Durham). Like *L. sericata*, the two are relatively commoner during the sheep-maggot season, i.e. mid-June to mid-September. The midsummer increase is more pronounced than the table indicates, as the proportions for the May-early June period are distortedly high due to the abnormally high *Lucilia* catch during the trapping period 5-9 June 1950—77% of 2243 flies.

(4) There is a marked sex disproportion in the trap catches, females being

greatly in excess of males in all species except *Phormia terrae-novae* R.-D. and *Cynomyia mortuorum* L. This sex difference in numbers responding to bait varies between species and according to season. Thus, with *Calliphora vomitoria*, *Cynomyia mortuorum* and to a less extent with *Calliphora erythrocephala*, males were relatively more numerous in mid-season; with *Lucilia caesar* they were most numerous in early summer. The sex-ratios of flies caught are of course no criterion of the absolute ratios, since females would be expected to respond more to meat stimulus, both gravid as well as hungry individuals being attracted.

(c) *The rise and decline of seasonal activity*

In 1953 serial trapping was carried on continuously from February to mid-May. A female *Calliphora erythrocephala* was caught in mid-March and four more during the following thirty days. From mid-April on catches gradually increased, including an occasional *Lucilia caesar* or *L. illustris*. Catch details in five-day periods from 17 April to 21 May, when trapping was discontinued, are given in Table 3. Graham-Smith (1916) in Cambridge found the order of first emergence

Table 3. *The species-pattern at the beginning of the seasonal activity curve, based on five traps*

	L.c.		*L.ill.*		*C.e.*		*C.v.*		*Cyn.*	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
17-21 Apr.						5				
22-26 ,,					1	6				
27 Apr.-1 May						8				
2- 6 May					28	78			1	5
7-11 ,,				1	40	292		2		2
12-16 ,,			1		11	64		1		
17-21 ,,	7		3	7	30	255		6		1

to be *Calliphora erythrocephala*, *C. vomitoria*, *Lucilia caesar* group and *L. sericata*. In his observations the males predominated in emergences of *Calliphora erythrocephala* up to May, although the sex ratio at emergence over the season was approximately unity. The all-male *Lucilia caesar* catch and relatively high *L. illustris* ratio in Table 3 may similarly indicate merely an earlier emergence of males. But it is to be noted that the presumably male-dominated early *Calliphora erythrocephala* population was represented by a low sex ratio in trap-catches. The marked differences between Tables 3 and 4 in the sex ratios of the *Lucilia* spp. caught may thus be further support to the suggestion in Table 2 of a seasonal difference in the population sex-ratio of *L. caesar*.

In October 1953 at the conclusion of a capture-recapture experiment on Crosby heavy trapping was continued until 17 November with 126 spherical gauze traps baited with rabbit. The traps were changed and the bait renewed every two days. The total catches per two-day period are given in Table 4. The *Lucilia* spp. ceased appearing by the end of October, and *Cynomyia mortuorum* very shortly after. *Calliphora erythrocephala* was being recovered in numbers up to

the end of trapping, but *C. vomitoria* was relatively rare after the end of October. This shorter activity season for *C. vomitoria* than *C. erythrocephala* was also commented on by Wardle (1927) under industrial conditions. The foregoing results bring out the important fact that *C. erythrocephala* was the predominant species on Crosby at all seasons, and the only species occurring in any numbers for several weeks at the beginning and end of the activity season.

(*d*) *The composite picture from other trapping experiments*

The above picture of the species pattern and its seasonal changes is supported by the massive if less critical evidence from other work. Various experiments were carried out at Crosby during the period 1949-53, mainly in connection with ground distribution studies and the standardization of methods. In these different baits were used, principally rabbit, herring and haddock. The relative proportions

Table 4. *The late-season pattern: total catch from 126 traps*

	L.c.		*L.ill.*		*L.amp.*		*L.sil.*		*C.e.*		*C.v.*		*P.t-n.*		*Cyn.*		Total
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
12 Oct.	2	112		235		5		3	619	14 489	12	1 064		1	9	33	16 995
14 ,,		5		3					37	2 379	2	37		1	2	9	2 493
16 ,,										89					1	1	91
18 ,,		65		85		2		1	337	13 334	18	613			1	31	14 487
20 ,,				9					13	2 186	1	85			1	6	2 301
22 ,,		25		47					336	7 245	7	485			4	13	8 162
24 ,,		1		2					73	3 810		25				5	3 916
26 ,,									16	2 101		10				2	2 129
28 ,,		1							132	3 190	3	23				5	3 354
30 ,,		1							93	2 181	2	5				1	2 293
1 Nov.										662		2					664
3 ,,									71	1 739		10			1	2	1 823
5 ,,									9	138		3					150
7 ,,									1	165		1					167
9 ,,										36							36
11 ,,									12	192							204
13 ,,									31	530							561
15 ,,									1	125		1					127
17 ,,									2	212		1					215

of species and of sexes attracted by different baits may differ appreciably. It also appears (Cragg & Thurston 1950, Williams 1954) that for any one species the relative attraction of different baits may vary with season. The tests were not evenly distributed seasonally, a disproportionately high number being made in the later part of the season. Nevertheless the pooled results for all tests (Table 5) confirm the general picture presented above of a species pattern consisting predominantly of *C. erythrocephala*, with *C. vomitoria* representing only 5% or less, and the remainder being almost entirely *Lucilia caesar* group (*L. caesar*, *L. illustris*, *L. ampullacea*). *L. sericata*, *L. silvarum* (included in the *caesar* group in the table), and *Phormia terrae-novae* each represented at most 1% or so, usually much less, and *Cynomyia mortuorum* was only slightly more numerous. The ratio *Lucilia* species : *Calliphora* species (*L* : *C* ratio) shows the mid-season increase in

the proportion of *Lucilia* species, and their virtual disappearance from the population by October. The ratio of *L. sericata* to the *caesar* group is given also, to underline the relative scarcity of this, the main myiasis-producing species, and its restriction, in the Crosby area at least, mainly to the July-August season. This is the more interesting in view of the fact that sheep myiasis may occur fairly frequently by late May, is common in September, and may continue well into October. The results given by Morison (1937) for traps distributed representatively in a sheep farming district in Aberdeenshire indicate a higher but still relatively low *L. sericata* proportion, viz. *L.s.* : *Lc.*gp. 0·09 : 1 in 1933, and 0·3 : 1 in 1934.

The preponderance of *Calliphora erythrocephala* in the Crosby blowfly population is consistent with the findings of Graham-Smith for country conditions in Cambridge and those of Wardle for the Manchester industrial area. It is in marked contrast, on the other hand, to the *L* : *C* ratio of approximately 8 : 1 reported by Green (1951), and Green & Kane (1954) for London slaughter-houses and domestic refuse depots respectively. The basis of their estimates is, however, not stated, and the results may not be comparable with trapping results.

Table 5. *Pooled catches from all experiments: Crosby 1949-53*

	Total	Percentage of catch							
		*Lc.*gp.	*L.s.*	*C.e.*	*C.v.*	*P.t-n.*	*Cyn.*	*L.s.*/ *Lc.*gp.	*L* : *C* ratio
To end of May	5 119	10	0·08	86	2·52	–	0·79	0·008	1 : 8·6
June and early July	14 885	35	0·63	61·3	1·7	0·38	1·06	0·018	1 : 1·8
July to 1st wk. Sept.	15 536	30	1·18	65·4	1·7	0·39	0·91	0·037	1 : 2·1
Sept. to 1st wk. Oct.	47 405	7·73	0·104	85	5·4	0·03	1·55	0·015	1 : 11·5
Oct. on	70 064	1·0	Nil	95	3·9	0·01	0·02	–	1 : 99

That the above picture is not peculiar to Crosby is shown by the species distributions obtained in three other areas (Table 6). The Breaks Moss, a reclaimed island of inferior grazing in an upland *Calluna* bog two miles north of the Crosby area, was sampled at irregular intervals over three years. The *Lucilia* species here were relatively fewer than on Crosby, and *Phormia terrae-novae* and *Cynomyia mortuorum* better represented. *Lucilia sericata* was scarce here also, the highest level for the ratio *L. sericata* : *caesar* group being 0·04 : 1, yet myiasis by this species during the three years was common. Mosspaul, an area of upland grazing on the Dumfries-Roxburgh border, was the venue of an experiment in 1953. On this high ground, ranging from 700 to over 1000 ft, the *Calliphora* species include a much higher proportion of *C. vomitoria*. *Phormia terrae-novae* and particularly *Cynomyia mortuorum* are distinctly more numerous relatively, but *Lucilia sericata* is still rare.

Consequent on the transfer of the laboratory, trapping was begun in 1954 in the low, wooded estuarine marsh of the Solway. The experimental area, Harker

Moss, is a limited area of uncultivated land among rich pasture land. It consists of a central raised bog merging, on different sides, into *Juncus* swamp, scrub, and cultivated fields. Trapping was done in July and early August, and this may account in part for the high $L : C$ ratio. The increase of *Lucilia* species did not embrace *L. sericata*, which remained as in the other areas well under 1% of the population.

The tent-trap catches on Crosby and the Breaks Moss, pooled like the bait-trap results without weighting for disproportionate frequency of habitat, are given in Table 7, and the relative proportions of species estimated from them. Though the trapping was obviously not representative (note the *Calliphora erythrocephala* sex-ratio in the Breaks Moss) and though the estimates are not necessarily any better than those based on the bait-trap catches, nevertheless they are independent, and the general agreement between the two suggests that the bait-trap

Table 6. *Total catches from different experimental areas*

	Total	Percentage of catch							
		*Lc.*gp.	*L.s.*	*C.e.*	*C.v.*	*P.t-n.*	*Cyn.*	*L.s.*/ *Lc.*gp.	*L* : *C* ratio
Crosby	153 000	9·7	0·22	85	3·9	0·09	0·6	0·02	1 : 9
Breaks Moss	10 000	4·8	0·1	82	12·0	0·3	1·2	0·02	1 : 19
Mosspaul	12 000	12·0	0·17	54	26·0	1·7	6·7	0·014	1 : 6·6
Harker Moss	8 400	49·0	0·25	35	14·0	1·5	0·25	0·005	1 : 1

estimate is not excessively biased by differential attraction to bait between the species. The 1952 results for Crosby were obtained in two comparable series of tent-trappings, in July and in September-October. In the table the totals for these two series are given. They illustrate the late-season decline in the $L : C$ ratio, as obtained with bait-trapping, and suggest that this is a true population effect. The two series show discrepancy in the sex ratio of *C. erythrocephala*, and possibly of the *caesar* group, suggesting either a seasonal decline in the ratio, or a seasonal difference between sexes in resting habitat.

NUMBERS AND SPECIES PATTERN IN RELATION TO THE BIOTIC ENVIRONMENT

Since the essential community relationship of blowflies is blowfly—small animals—vegetation, the numbers of flies must finally be determined by the availability of food and shelter for adults in the vegetational habitat and of carrion for survival of the species. It is a matter of common observation that the fly population is not uniformly distributed; the apparent fly-density in major fragments of the general environmental mosaic tends to differ where these fragments are markedly different, e.g. wooded valley, open hill slope, marsh and grazing fields. Though this association of numbers with environment is evident, it by no means follows that the adult flies will be distributed in any quantitative

relation to an element of this environment. Thus the scale of microgeographical variation in distribution of carrion might not coincide sufficiently with the territorial range of flies to cause appreciable grouping of the adult population, even though the density of carrion primarily determined the level of the population. Similarly with the vegetational habitat. The Calliphorinae are powerful and generally active flies able to travel above the field-layer and probably the low-canopy-layer, their flight to a large extent independent of the vegetational habit. Further they are not physically restricted to a limited distance range, and individuals have flown at least a mile in a matter of hours (unpublished work). The fact has to be faced that in the present state of our knowledge there is nothing to indicate whether the non-uniform distribution of the adult population is due to the faunal, floral, vegetation-structural or edaphic element of the environment, or to some combination of these.

Table 7. *The species-pattern as shown by tent-trapping*

(+*x*) indicates records for which the sex is not known

	Total	*Lc.*gp.	*L.silv.*	*L.s.*	*C.e.*	*C.v.*	*P.t-n.*	*Cyn.*	*L* : *C*
CROSBY									
July 1952 ♂/ ♀	(51)	5/2			9/33		–	2/–	1 : 6
Sept.-Oct. 1952 ♂/ ♀	(33)	–/1			1/26			1/4	1 : 27
Total	(148)	6/6(+1)	(+1)	1/1	26/87(+3)	5/4	–	3/3(+1)	1 : 8
%		9·5		1·5	79	6		5	
BREAKS MOSS									
Total ♂/ ♀	(54)	2/2	–/1	–	1/40	–	–/4	2/2	1 : 8
%		9			76		7·5	7·5	

In attempting a breakdown of the observed relation between variation in population-density and diversity of environment, we must make use of some descriptive term for the 'place' where a grouping of the population exists. The two ecological units of area already defined, the location and the subsection block, are not suitable for this purpose, being restricted to a degree of uniformity of vegetational composition; they are in fact units against which, among others, the 'place' may have to be matched for correspondence of population. The unit of fly-territory, which is arbitrarily defined as that amount of sub-aerial space which would contain two average-length bursts of flight, is not an ecological entity but merely a convenient measure of space for mathematical study of dispersal.

We shall adopt the useful concept of an 'arena of activity' (Elton & Miller 1954) defining it at this stage merely as that part of the general habitat in which a fly tends to spend more time than would normally be occupied in traversing it in the course of random flight movements. Since this slowing-up of individual passage will result in population grouping, it follows that the population-density in arenas of activity will vary according to the extent to which individual flies

loiter in them. This basic definition does not prejudice the question of what causes the loitering, or whether the aggregation is permanent or ephemeral. It is useful also in that it will not be affected by future clarification of the nature of individual movement; a population peak in an activity-arena may equally well be imagined as mainly of the same individuals, or a continuously changing succession. A crowd is a fact irrespective of whether it is at a city turnstile or in a village pub.

We may now examine the bait-trapping and other results for evidence of a mosaic pattern in the spatial distribution of blowflies, and in this preliminary account shall confine ourselves to the relation of distribution to vegetation-type and structure. It should perhaps be emphasized again that these bait-trap results indicate the numbers and species-composition of concentrations of flies attracted to bait placed in different vegetational associations; from how far and from what variety of vegetational haunts they have been attracted the catches give no indication. For the present we must assume that the experimental distribution of carrion baits does not accelerate the normal rate of transgression of arena boundaries by individuals of the population to the extent that the identities of the population groupings are destroyed.

(*a*) *Serial trapping results*

As previously stated the five traps used in the serial trapping on Crosby were used in five fixed positions. For classifying these and other later described habitats we have adopted the habitat-structure classification proposed by Elton & Miller (1954).

(1) Meteorological Station (Plate 4 *A*). Open-ground to field-type edge. A flat raised platform of *Agrostis* turf over an underground wartime 'operations room'. The platform was about 3 ft above the surrounding area which formed an open arena covered by an *Agrostis-Holcus* association, with an abundance of fescue and strong under-flora of *Lotus*, vetches and silver-weed. Arable ground lay adjacent to the east side.

(2) Water Tower (W.T.) (Plate 4 *B*). Field-formation to scrub-formation edge. This area was a narrow strip of field-margin alongside a road with hedges. The trap site was under an elevated water tank in a small patch of rushes to 2 ft with a tall growing (1 ft) *Equisetum* forming a dense and moist cover. To the south of the tower were strong rushes without *Equisetum*. In the shelter of the near hedge was a lush growth of Yorkshire fog, nettles, wood sage, thistle and knapweed. The hedge was holly and elder, with a straggling growth of bramble.

(3) Guardroom (G.R.) (Plate 5 *A*). Mixed field- and scrub-formation types. A sheltered site, protected to the north and east by hawthorn hedges and isolated trees with bramble undergrowth, and by buildings to the south. Arable fields lay to the west, and, beyond the hedge, to the north. The field layer was rank pasture, uneven but not tussocky, of *Holcus-Agrostis* with a straggling growth of bramble invading from the hedge, and *Lotus* among more lush grass. There was

A. The Meteorological Station site. *Holcus-Agrostis* to the north (right foreground); growing corn crop to east and south.

B. The Water Tower site, looking north. The trap site was in the rushes underneath the raised water tank; beyond the buildings lies the Guardroom site.

(*Facing p. 148*)

A. The Guardroom site. The trap was stationed beyond the first telegraph pole.

B. The Reservoir site (foreground). The Wood site was in the scrub beyond the building.

(*Facing p. 149*)

frequent occurrence of casual herbs, e.g. water parsnip, knapweed, ragwort, plantain and also thistle and nettle. About 20 yd away, across the hedge to the east, lay an overrun duckpond.

(4) RESERVOIR (Res.) (Plate 5 *B*). Field-formation type, with high field-layer. This site was an *Agrostis-Holcus* association fragment with diffuse growth of whin and some low bramble and solid stands of willowherb. Around a static water reservoir was a strong diffuse growth of rushes.

(5) WOOD. Low-canopy deciduous woodland-formation type. Adjacent to and north of the Reservoir site was a wood of regenerating birch saplings to about 20 ft. There were a few trees, and occasional small clearings. Along the wood margin were banks of broom. There was a notable growth of buckler fern associated with the *Holcus* field-layer of the clearings, and of hard fern associated with the wavy hairgrass which formed a close mat under the scrub birch. The trap site was some 30 yd from the south edge at the extremity of an overgrown re-entrant clearing with characteristic extensive growth of willowherb and bramble.

Table 8. *Crosby serial trapping results in relation to trap site*

Percentages of the catch in parentheses

Site	Total	*L.c.* ♂/♀	*L.ill.* ♂/♀	*L.amp.* ♂/♀	*L.s.* ♂/♀	*L.silv.* ♂/♀	*C.e.* ♂/♀	*C.v.* ♂/♀	*P.t-n.* ♂/♀	*Cyn.* ♂/♀
Met.	837	–/8 (0·96)	5/83 (10·51)	–/1 (0·12)	1/15 (1·91)	–/4 (0·48)	98/610 (84·47)	–/4 (0·48)	–/2 (0·24)	–/6 (0·72)
W.T.	1 812	4/137 (7·78)	7/185 (10·59)	–/2 (0·11)	–/7 (0·39)	–/21 (1·16)	64/1357 (78·42)	–/18 (0·99)	–	–/10 (0·55)
Res.	1 542	11/167 (11·54)	26/316 (22·18)	–/7 (0·43)	–/24 (1·56)	4/58 (4·02)	121/702 (53·37)	23/63 (5·58)	4/3 (0·43)	5/8 (0·84)
Wood	2 159	60/163 (10·32)	47/208 (11·81)	3/109 (5·19)	–/1 (0·05)	–/21 (0·97)	309/1118 (66·09)	27/88 (5·33)	4/– (0·18)	–/1 (0·05)
G.R.	1 461	26/208 (16·02)	64/319 (26·22)	–/4 (0·27)	1/4 (0·34)	–/22 (1·51)	109/670 (53·32)	4/26 (2·05)	–	2/2 (0·27)

The five sites were all within the 'Lab. Section' (see later) and lay within an ellipse no more than 150 yd long. The Wood and Res. sites were only some 40 yd apart.

The pooled results for 1949-52 for each site over the period mid-June to mid-September are given in Table 8. They show that within 150 yd range a difference in catch of almost three to one may occur between two traps; further, the catch level seems to be related to the structure of the ground cover, the two extremes, Wood and bare Met. Sta., having the highest and lowest respectively. Over the whole season the catches show a rather different distribution between the sites, the W.T. having the highest catch with the G.R. next; these relative proportions are, however, unduly influenced by the *Calliphora erythrocephala* component, since the early and late catches consisting predominantly of this species formed more than half the total (see Table 2). The species pattern also differs between sites. The *L* : *C* ratio is 1 : 6 for the Met. Sta., but over 1 : 2 for the rough mixed growth of the G.R. and Res. sites.

Lucilia sericata is apparently a fly of open or low-field-layer haunts; it was more numerous, both relatively and absolutely, in the Met. Sta. and Res. than in the other sites. The preference of the species for open conditions is also brought out in Morison's results in Aberdeenshire and those of Cragg (1950) in Denmark. It may be associated with the greater insolation, as suggested by Holdaway (1933) and not with the vegetation type or structure. The *caesar* group on Crosby, unlike *L. sericata*, was commoner in the canopy-layer and tall-field-layer sites, the three species showing a gradation from the extreme wood-association of *L. ampullacea* to the relative indifference to degree of cover of *L. illustris*, which was as numerous as *L. caesar* in the Wood site trap, twice as numerous in the Res. trap, and ten times as numerous in the Met. Sta. trap.

Calliphora erythrocephala appeared in greatest relative numbers on the Met. Sta., and in greatest absolute numbers on the relatively open W.T. site. *C. vomitoria* on the other hand favoured the Wood site and the high-field-layer Res. site adjacent to it. Wardle (1927) makes the suggestion that failure to take the latter species in traps in the open is due not so much to its absence from such habitats as to its higher threshold of response to carrion odour; the rapid desiccation of baits in unshaded situations results in low or nil catches.

The male : female ratio of those species of which adequate numbers were caught (*Lucilia caesar*, *L. illustris* and *Calliphora erythrocephala*) was higher in the sites with continuous or interrupted canopy-layer, the Wood and G.R., than in the sites with field-layer only. The limited evidence for *Phormia terrae-novae* suggests that the same may be true of this species. Since the bait was standard, differences in ratio of trapped flies are probably related to differences in the actual ratio of the population, i.e. the sexes would appear to be differentially distributed in relation to vegetation cover. An alternative explanation is that the males, which appear from the low numbers trapped to be relatively uninterested in carrion, only visit traps which happen to be within their activity-arenas, whereas females are drawn from other arenas. This implies, however, that canopy habitats are preferred by the three species in question, an assumption not borne out by the *Calliphora erythrocephala* catches.

(*b*) *Differences between sections*

Blowfly population studies on the Crosby experimental area have been made mainly on four sections—the Laboratory, the Scrub, Modlin's and Beanlands. We shall briefly describe these four sections and their subsections; experimental results will then be examined for evidence of differences in the numbers and species-pattern of the blowfly populations, firstly between sections, i.e. between moderately large areas some distance apart, and secondly between their subsections, quite close together and sometimes actually contiguous. The sections lay near the perimeter of the aerodrome and represented the corners of a rough parallelogram with sides varying from about ¼ to 1 mile.

(1) The Laboratory Section contained the five serial trapping sites already

described, and consisted of four subsections: (i) The Wood, already described; (ii) the Lab. subsection, a rectangular area extending east from the Res. site. The *Agrostis-Holcus* association at the latter site extended over the whole subsection, but the structure changed eastwards from tall field-layer to low, the clumps of whin being confined to the neighbourhood of the Res. site, and the willowherb and rushes being decreasingly present eastwards. (iii) The Hedgerows. These bounded the section to the north-east and north-west, and included the W.T. and G.R. sites. The formation-type was for the greater part scrub-edge, but included a group of buildings and occasional isolated trees. (iv) The Fields. These lay between the Lab. and Hedgerows subsections, and extended to the Wood. Ley grassland or oats, they were sampled only as aftermath or stubble, i.e. when structurally they represented open-ground formation-type.

(2) THE SCRUB SECTION consisted of three sub-sections: (i) The Scrub sub-section, structurally not scrub type, but a field-formation with tall field-layer. It formed a peninsula of relict scrub extending into arable ground. The cover consisted of isolated bushes of birch, and occasionally willow, usually under four feet, on a dry heath of mixed heather, rushes (*Juncus squarrosus*) and *Polytrichum commune* with some *Agrostis canina* and Yorkshire fog. Contributing to this structure were willowherb, broom, whin and bramble, giving the complex its characteristic low scrambling life-form. (ii) The Gorse subsection, a field-formation-type, with tall field-layer. This was an island of dry sward between two roadways. The tall field-layer was open diffuse broom, on *Agrostis alba* sward, with associated abundant *Juncus squarrosus*, tormentil and frequent heather and whin. (iii) The Bleatarn subsection. Structurally a wood-edge formation-type, this ecotone bordered a narrow extension northward into the aerodrome of a peripheral beechwood regenerating sycamore. The dominant field-layer of the wood, willowherb, bramble, and nettles, with false oat-grass, extended outwards to form a ten-foot margin. Beyond this, at the north-east corner, was a solid stand of broom, 6 ft tall, with a ten-foot-broad belt of solid bracken continuing southward and tending to invade the wood margin.

(3) THE MODLIN'S SECTION. This was a rectangular field, approximately 150 by 50 yd, forming part of a narrow strip of ground between the perimeter road of the aerodrome and a highway with hedges on the south side. Beyond the highway lay fields and a wood. East of the section was an uncultivated area of waste-land with rank growth, but the ground to the west and north was cultivated.

(4) THE BEANLANDS SECTION. This was roughly comparable vegetationally to Modlin's. It consisted of the ten-foot marginal strips of grass border between the perimeter road and cultivated ground on the one side, and rank herbage on the other. It was regarded as corresponding more to a subsection than a section complex, but did not have the same degree of vegetational uniformity as Modlin's.

The study of these sections was not complicated by distribution and movements of domesticated animals. A few sheep grazed on the Scrub section in late summer and autumn of 1950 and 1951, otherwise the actual sections were free of stock. There were usually cattle in nearby fields to the north-east and north-west of

the Lab. section, and to the south of Modlin's. Occasionally, sheep and cattle grazed fields nearby Beanlands. Up to 1953-54, rabbits were very numerous on the Scrub section, and, to a lesser degree, on the Lab. section. Beanlands and Modlin's were largely free of warrens, though grazed by rabbits from nearby fields or hedgerows; presumably therefore the carrion population was less on these two sections.

Little of the tent-trapping work on Crosby was designed for comparison of areas, but the meagre results available are perhaps worth passing mention. In

Table 9. *Details of release-recapture experiments in 1951*

	August			September		
	Released	Recovered	Total samples	Released	Recovered	Total samples
BEANLANDS						
Total	241	7	1 349			
*Lc.*gp. males	7	1	84			
*Lc.*gp. females	17	1	387			
C.e. males	37	0	142			
C.e. females	174	4	686			
Others	6	1	50			
SCRUB						
Total	270	16	1 314	353	7	2 901
*Lc.*gp. males	15	1	88	3		9
*Lc.*gp. females	50	2	365	53		187
C.e. males	47	1	282	50	0	213
C.e. females	151	10	545	204	5	2 216
Others	7	2	34	43	2	276
MODLIN'S						
Total				278	4	4 123
*Lc.*gp. males				0		0
*Lc.*gp. females				14		130
C.e. males				38	0	291
C.e. females				214	3	3 492
Others				12	1	210
LAB.						
Total				1 002	54	10 486
*Lc.*gp. males				6	0	30
*Lc.*gp. females				74	3	347
C.e. males				186	7	1 596
C.e. females				642	42	7 458
Others				94	2	1 055

1952 the Lab. and Scrub sections were trapped in July and in September-October. Four tents per location were put out on twelve occasions, but the numbers of locations per section were not kept equal. In July 240 m^2 on the Lab. section yielded 21 blowflies, and 116 m^2 on the Scrub 3 blowflies. In September-October, the Lab. section figures were 14 flies for 314 m^2, and the Scrub 16 flies for 216 m^2. The Lab. section thus shows a decline, between the summer and autumn, from approximately 350 flies to 175 flies per acre, whereas the Scrub section density rises from 80 to 290 flies per acre. In certain experiments in 1949 pairs of tents were put on five locations on the same two sections. These ten locations were trapped simultaneously on twelve occasions during July and August, i.e. 120 m^2 of each section were trapped. The Lab. section yielded three

blowflies, while the Scrub yielded six. These catches, if representative, would indicate densities of 100 and 200 blowflies per acre. The sampling error is of course very high with such low numbers, but the results suggest two conclusions: that the blowfly population may be in the order of only a few hundred flies per acre; and that not only may the density differ between sections, but also the nature of the change in density in a given period, i.e. one section may show increase over a period during which another is declining.

In August 1951 in a small scale test of the release-recapture method flies were marked and released on the Scrub and Beanlands sections. Samples were trapped on the two sections on three successive days. The flies were chilled, individually paint-marked, using a different colour each day, and released in the evening. (For details of technique see MacLeod & Donnelly 1957.) Recovery trapping continued for eleven more days. In September three sections, the Lab., Scrub and Modlin's, were compared in a second marking experiment. Five groups were

Table 10. *Population estimates per acre from the 1951 release-recapture experiments*

Higher values are smoothed to nearest 5; values in brackets are estimated from ratio 1 male to 3 females —

	August		September		
	Beanlands	Scrub	Scrub	Modlin's	Lab.
Total	230	95	455	845	660
Calliphora erythrocephala					
Males	?	?	?	?	130
Females	135	33	305	725	370
Total	195	60	(400)	(960)	495
C. vomitoria					
Females					110
Lucilia caesar group					
Females	?	?	?	?	52
Total	34	43			

released on each section over a period of eight days, recovery trapping continuing for nine further days. Details of the two experiments are summarized in Table 9. The results of these two experiments were inadequate for examination by the method of Dowdeswell, Fisher & Ford (1940), and only a crude analysis has been made by the following simplified method. The estimated number of each release available each day is calculated taking into account mortality and recaptures. From these the total of all releases available on each day is obtained and converted into a mean number available over the trapping period. The total samples, total recoveries, and this mean number available give an 'estimate from pooled results' of the population. For the August test 2% mortality per day of marked flies was assumed, and for the later test, 4%.

On the assumptions that the 'unit of territory' to accommodate random oscillation of individuals has a radius of 100 yd and that the zone of influence of traps distributed over a unit of territory extends half way across adjacent units, the

area being sampled when a unit of territory (6-7 acres) is trapped, is approximately 25 acres. A mean value of 16% of released flies is assumed as the proportion remaining in the 25 acres around the release point during the first week. The argument for this is given elsewhere (MacLeod, in preparation).

In the Lab. and Beanlands sections the traps were spread over 150 to 200 yd, i.e. a full unit of territory is assumed to be trapped. In the Scrub and Modlin's sections the trap groups were more compactly distributed, in each case occupying an area approximately 100 yd square. The zone of influence of the traps extending to 150 yd radius is thus approximately 15 acres. For convenience, the first density contour of distribution is imagined to be two territory units from the centre of a concentration, i.e. the distribution curve is only negligibly higher in the central than in the adjacent units. In such case, 10% of the released flies ($15/25 \times 16$), are within the zone of influence of the traps. On the above basis the density of blowflies per acre for the different sections has been calculated in Table 10. In the Lab. section in September 7 male and 42 female *Calliphora erythrocephala* were recovered. Estimated separately for the sexes, the populations are 130 males and 370 females. Taking 1 : 3 as an estimate of the true sex ratio in September, the *C. erythrocephala* populations on the Modlin's and Scrub sections may be estimated (Table 10). The August estimates of *C. erythrocephala* on the Scrub (1 male and 10 females recovered) give a sex ratio of 55 to 32. Though the estimate from the single male recovery has very wide confidence limits it indicates that the sex ratio in August is at least nearer unity than that found for the September assessment, where the population was probably changing towards the pattern for the late-season decline. The female estimate for Beanlands is 134 as against the unsexed estimate of 194, again suggesting a higher male : female ratio than the September ratio of 1 : 3.

Although the recoveries for the *caesar* group are all low, the consistency of the estimates, 44 and 34 on the Scrub and Beanlands in August and a female estimate of 52 for the Lab. section in September, suggests that they are at least an approximation. The *Calliphora vomitoria* estimate on the Lab. section is based on two females recovered. Only single recoveries were made of *Lucilia sericata* and *Cynomyia*, but it is at least suggestive of very low population densities for these two species that only this one *Lucilia sericata*, and only four *Cynomyia* were released in the Scrub section, in which the recoveries were made, and that the recovery samples were only 7 and 6 respectively.

Because of the low frequency of recoveries and the failure to obtain re-recaptures, the method of successive releases gave results difficult to interpret. In a test on the Lab., Scrub, and Modlin's sections in October 1953 a single large release was made. Groups of approximately 1000 flies trapped on the sections were fed with radioactive phosphorus and released in their own sections. The catch at this season contained relatively low numbers of species other than *Calliphora erythrocephala*, and so limited numbers of laboratory-bred *Lucilia sericata*, *L. caesar* and *Phormia terrae-novae* were added to the wild material. Occasional recoveries were made up to the twenty-fourth day, but, for purposes

of assessing the population density, only the recoveries during the first week are considered. The net daily number of available flies has been calculated by deducting recaptures and 4% for deaths from the proportion of the releases assumed to be within the zone of influence of the traps. In this experiment the traps on the Scrub, as well as those on the Lab. section, occupied a unit of fly territory; on Modlin's they were restricted as in 1951 to an area approximately 100 yd in diameter. Details of releases, and the resulting estimates, are summarized in Table 11. Neither unmarked nor marked *Lucilia sericata* were caught and only 1 *Phormia*, a marked specimen. It is probable that seasonal conditions resulted in the laboratory-bred material of these two species dying during the first night, or at least being immobilized subsequently. For the same reason the estimate from the mainly laboratory-bred *Lucilia caesar* is suspect, as the actual numbers

Table 11. *Release-recapture experiment, October 1953*

Estimates for total blowflies, for males and females *Lucilia caesar* and for females and total *Calliphora erythrocephala*. (Numbers expressed as males/females)

	P.t-n.	*L.s.*	*L.c.*	Other *Lucilia*	*C.e.*	*C.v.*	*Cyn.*	Total
LAB. SECTION								
Released wild	–	–	–/2	–/2	19/1 083	1/28	–/5	1 140
Released lab. strain	30/29	10/5	52/17	–	–	–	–	143
Recoveries	–	–	1/9	–	–/88	–	–	98
Total samples	–	–	2/88	–/112	272/11 697	12/653	2/18	12 856
Estimates/acre			0·27/0·65		?/732 (Total 760)			761
MODLIN'S SECTION								
Released wild	–	–	–/12	–/21	8/741	–/7	1/10	800
Released lab. strain	11/11	15/7	75/23	–	–	–	–	142
Recoveries	–/1	–	3/13	–	–/30	–	–	47
Total samples	–/1	–	4/72	–/120	327/7 910	6/337	8/23	8 808
Estimates/acre			0·16/0·70		?/956 (Total 1 008)			724
SCRUB SECTION								
Released wild	–	–	1/7	–/12	25/980	–/22	1/10	1 058
Released lab. strain	25/25	12/6	61/21	–	–	–	–	150
Recoveries	–	–	3/19	–	–/56	–	–/2	80
Total samples	–	–	5/57	–/104	394/10 684	14/724	4/33	12 019
Estimates/acre			0·21/0·18		?/964 (Total 1 024)		?/4·5	815

available may have been considerably less than those calculated. The low recovery totals for males make their estimates very unreliable, but even assuming sex equality in numbers the density is still under 2 per acre on all three sections.

In view of the probable loss by death of much of the laboratory-bred material, the total calliphorine population is estimated on the wild material only. No male *Calliphora erythrocephala* was recovered, and as the catches were very predominantly female, the estimate for combined sexes is very close to that for females. Two of the ten female *Cynomyia* releases on the Scrub were recovered. This is a lethargic species, and unlike the others is believed not to travel far from the point of release. The estimate is therefore made on the assumption that all the marked group remained in the 25-acre zone of influence of the traps.

Before reviewing the results in Tables 10 and 11, it is necessary to point out a source of error in Lincoln-index estimates of numbers, where the population is heterogeneous. If the constituent elements of the population are for any reason disproportionately represented in the marked sample, then it is essential that recovery samples have the elements in proportion to their numbers in the population, not as in the marked sample. Now, if one sex were relatively less attracted to meat than the other, a bait-trapped sample for marking would naturally reflect this and the males would be disproportionately few. It can readily be shown that if this same bias recurs in recovery samples, though the separate estimates for sexes are not affected, that for combined sexes will be low. The *Calliphora erythrocephala* estimates for the Lab. section in September (Table 10) show only negligible difference between the sum of the sex estimates and the estimate for combined sexes. This might seem unexpected, in view of the fact that the sex ratio attracted to bait is usually much lower than the estimated 1 : 3 (cf. Table 2). It will be seen from Table 9, however, that the sex ratio in the released samples was in fact unusually high compared with that of the later recovery samples, and also with the ratios on the other sections. The converse case where the marking sample disproportion is inverted in the recovery samples will result in an exaggerated estimate. This effect is more unlikely in practice than the former, but can in fact be demonstrated from the present results. The summed estimates for sexes of *Lucilia caesar* (Table 11) are 0·92, 0·86 and 0·39. If the estimates were calculated on the total *L. caesar* release and recovery, they would be 2·8, 1·84 and 0·74. In this case the marked sample was added to the population, and contained an excess of males. The recovery sample, being bait-trapped, had a high and presumably disproportionate excess of females. The mathematical result of these opposing disproportions is an over-estimate.

The population estimates in Tables 10 and 11 show marked discrepancy between those for the first experiment in August and the later two in September and October. It is, of course, possible that the population did actually vary as suggested by the results, but it is more probable that bias has occurred in the sampling. The August results are supported by the tent-trap estimates, but on the other hand the later-season results for 1951 and 1953 are not inconsistent with each other.

As indicated above, with heterogeneous material disproportionately sampled both for marking and in later recovery trapping, a 'total Calliphorines' estimate will be low. The October samples approached more to pure *Calliphora erythrocephala* catches than did the other two sets, and this is probably reflected in the greater uniformity of the section estimates. The higher estimate for *C. erythrocephala* females alone than for total Calliphorines on two of the sections suggests, however, that the latter have been under-estimated, from differential response of species or of the sexes of each species. Although the estimates for different occasions cannot be taken as comparative, those for the different sections for each occasion should be to some extent comparable. They suggest the following inferences: that sections may differ markedly in blowfly densities (e.g. 1951) or may be relatively uniform (1953); that differences in density need not necessarily

affect all of the component species (e.g. Beanlands and the Scrub, August 1951); that the sex ratio at a given season may vary between sections (e.g. 1953, *L. caesar*); that the numbers of *L. sericata* and *P. terrae-novae* are relatively very low on Crosby, and *Cynomyia* also, though possibly more numerous than these, forms only a small proportion of the total Calliphorine population, which is made up predominantly of *Calliphora erythrocephala* and the *caesar* group, with *C. vomitoria* possibly a third major element. The earlier decline of the *Lucilia* spp. than of *Calliphora erythrocephala*, shown in bait-trapping results, is apparently a true population effect, and not a seasonal change in degree of response to bait (cf. September 1951 and October 1953, and also the $L : C$ ratios for August and September).

The initial and recovery samples for the release-recapture tests provide material for direct comparison of the population responding to bait-traps in each section. By pooling the catches over successive days, a more reliable estimate should reasonably be expected, provided the number of traps is not such that the population level is being sensibly diminished each day, and, further, that the daily trapping of the area does not result in an induced pattern. There is no evidence that with small numbers of traps, such as were used in the 1951 tests, the population pattern or level is affected. The first week's catches in the August experiment were therefore pooled by sections. The Scrub was sampled by eight traps, Beanlands by twelve. The pooled catches are shown in Table 12. In the September test, the Scrub was sampled by twelve traps, and the Lab. and Modlin's sections by sixteen traps each. The numbers caught, both in absolute numbers and in relative proportion between the three sections, showed a marked change during the recovery trapping period. The catches for the first three days and for days 5 to 9 have been pooled separately (Table 12).

In the August results (first two lines of table) the mean catch per trap on the Scrub section is nearly twice that for Beanlands, and this difference is consistent for the major species groups (but not for *Lucilia sericata*). The first comparison of the three sections tested in September shows the highest catch on the Lab. section and the lowest on Modlin's (which was somewhat similar to Beanlands), the difference here also being consistent over the species pattern. But within a few days a striking change occurs in the *Calliphora erythrocephala* catch in all three sections; the Lab., still with the highest total, has trebled its catch per trap and Modlin's, with an even greater increase, now has a higher total catch than the Scrub. This rearrangement of ranking is not, however, consistent for species, and is due mainly to the greater increase of *C. erythrocephala* in the Modlin's catch than in the other two. The *caesar* group, and *C. vomitoria*, have increased only in the Modlin's catches.

The totals discussed above are derived from several days' trappings, and so the error to be attached is not readily obtainable. In the October 1953 experiment a massive single-day trapping was used for the initial sample for marking, the three sections being simultaneously trapped each with 84 traps. The total catches for these initial samples were: Lab. 4405, Scrub 3573, Modlin's 3045. The difference

Table 12. *Comparison of trap-catches on different sections*

Numbers caught are expressed as males/females

		Traps	*L.s.*	*Lc.*gp.	*C.e.*	*C.v.*	*Cyn.*	*P.t-n.*	Total	Mean catch per trap	*L* : *C* ratio
15 to 20 Aug.	Beanlands	12	1/21	52/239	151/618	1/3	2/4	–	992	11·8	1 : 2·4
	Scrub	8	/3	68/281	238/524	2/9	1/2	–	1 137	20·3	1 : 2·2
11 to 13 Sept.	Lab.	16	–	11/94	128/437	10/71	1/4	1/–	757	15·75	1 : 6
	Modlin's	16	–	–/15	16/72	–/3	1/1	–	108	2·25	1 : 6
	Scrub	12	–	6/74	21/128	2/15	5/4	–	255	7·1	1 : 2
15 to 19 Sept.	Lab.	16	–	8/80	410/1 400	18/85	6/17	2/2	2 028	42·25	1 : 22
	Modlin's	16	–/1	–/47	104/665	2/23	6/12	–	860	17·9	1 : 16·5
	Scrub	12	–/2	3/52	52/230	–/20	6/16	–	381	10·6	1 : 6

in catch per trap between the Lab. and Scrub sections, $9{\cdot}9 \pm 4{\cdot}8$, is significant at the 5% level. As in the September comparison, however, this ranking order is not permanent, even over a period of only a few days (see below).

Sections may also show differences in the species-pattern of the catch, and these differences may be reversed in late season catches. Thus, the $L : C$ ratio in the September catches is higher on the Scrub than on the other two sections (Table 12); in October the *Lucilia* species, though in very low numbers, showed a preponderance on the open-ground Modlin's: 4·3% of the total catch, as against 1·1 and 1·8% for the Lab. and Scrub. It is worth noting that the sex-ratio may also differ, the higher ratios being apparently related to greater cover, as canopy or tall-field-layer. Thus, the Scrub and Beanlands (Table 12) show different sex-ratios of *Calliphora erythrocephala* (1 : 2 and 1 : 4); the Lab. section has a higher ratio than the other sections in both the September groups of catches. The sex-ratio in the *caesar* group is also higher in the Lab. than in the other two sections in the September catches, but the catches are too low for the differences to be convincing.

For the recovery samplings in the October test forty-two traps were used per section. They were emptied and the bait renewed every second day. The first four recovery trappings gave the following totals, consisting almost entirely of *C. erythrocephala*: Lab.—5393, 1415, 58, 5982; Scrub—6993, 425, 18, 4576; Modlin's—4236, 635, 15, 3918. The Scrub had thus the highest catch on the first occasion, the lowest on the next, and was intermediate on the fourth, in each case the difference between it and the Lab. section being statistically significant. This day-to-day variation in the ranking order of the sections can scarcely be due to differential change in activity of the fly population between sections, since weather conditions were common to the three sections. Neither does it appear to be due simply to differences in activity-response between sections according to whether the change of weather is towards better or worse conditions for activity. Thus at the first and fourth recovery trapping, the mean catch on the Lab. section was two or three times greater than the mean initial catch, indicating similar weather conditions for these recovery dates; yet at the fourth trapping the ranking order for the Lab. and Scrub sections agrees with the order at the initial trapping, but is the opposite at the first recovery. Vegetational changes must be ruled out as a possible explanation of changes in relative catch-level over such short intervals of time. We must conclude therefore, at least for *C. erythrocephala*, that the association of ranking order of catch with the sections is inconstant over relatively short periods of time, that changes in relative distribution between sections may be a true population effect and not an activity effect, and that these population changes may be independent of change in vegetational environment. It might at first glance appear as if the first two above conclusions could be checked by examination of successive daily estimates of absolute numbers on the three sections. The use of the Lincoln-index for estimating day-to-day fluctuations from a single release is, however, unjustifiable, for two reasons: a sudden decrease of population cannot be revealed by the method, which will merely estimate the

same population as before the catastrophe, and apparent decreases may be suggested by successive estimates, but the acceptance of these requires the biologically improbable assumption that there has been either selective removal of unmarked flies or a surge of re-immigration of earlier emigrated marked flies. If such estimates of decrease are not accepted, however, then the estimates showing increases must equally be suspect.

Even apart from day-to-day variations in the absolute and relative numbers of flies in the sections, which may be due to the *C. erythrocephala* component only, there still appears to be an unexplained discrepancy between the estimated ranking order based on bait-trap catches and that based on estimates of actual numbers, even when confined to a single species. Thus, the *C. erythrocephala* estimate is higher for Beanlands than for the Scrub; the bait-trap samples give the reverse ranking. Similarly on Modlin's, this species is estimated as more numerous than on the other two sections in 1951, and equal in 1953; the bait-trap estimates ranked Modlin's as lowest in both years. It does not seem probable that traps would consistently catch the fewest flies on the section with the highest

Table 13. *Tent-trap results in relation to vegetation type*

Numbers caught are expressed as males/females

	July					Sept.-Oct.				
	Sq. m	*Lc.*gp.	*C.e.*	*Cyn.*	Total	Sq. m	*Lc.*gp.	*C.e.*	*Cyn.*	Total
LAB. SECTION										
Excl. Wood	200	–	1/12	2/–	15	260	–/1	1/3	–/1	6
Wood subsection	40	–	–/6	–	6	54	–	–/8	–	8
SCRUB SECTION										
Scrub subsection	80	–	1/–	–	1	108	–	–/1	1/1	3
Gorse subsection	36	–	–/2	–	2	108	–	–/12	–/1	13
OTHER AREAS										
Aftermath	18	–	–/2	–	2					
Permanent pasture	56	1/–	5/4	–	10					
Tree	(5 occasions) *L.c.* –/1; *C.e.* 12/21; *C.v.* 5/2; Total 41									

population, and there is very probably a bias of estimate here, e.g. through the loss-rate of the marked group being underestimated. An exceptionally high emigration rate would be consistent with the low bait-trap catches, relative to those of the other simultaneously trapped sections; it could also account for the inflation, since it would result in reduced recoveries and a mistakenly high estimate of available marked flies. The discrepancies underline the need for a detailed examination of any relation which may exist between the character of the terrain and the rate of dispersal of fly concentrations.

(*c*) *Differences within sections*

So far we have considered differences between sections on the implicit assumptions that the populations within the sections were uniformly distributed, and that differences obtained could be related to the sections as a whole. We may

now consider to what extent the failure to elicit any clear pattern of difference may be due to essential heterogeneity of population on the section itself. Release-recapture estimates are obviously inapplicable for comparison of limited adjacent areas. Also, the bait-trap method will be the less effective, the smaller or more closely adjacent the subsections being examined. The tent-trap method should be suitable for subsection comparison, but so far only some preliminary observations have been made.

In the 1952 experiments with tent-traps the tents were used in groups of four, each group being on a single mosaic fragment—a location. On the Scrub section, four locations were on the Scrub subsection, and four on the Gorse. One of the Lab. section locations was in a small clearing in the Wood subsection, the others being in the Lab. subsection. In addition to the locations on the two recognized sections, other locations were trapped in the July period, including two on a field of aftermath grass, and four on a field of *Agrostis* permanent pasture, occasionally grazed by cattle. A 'tree-tent' —a larger version of the standard tent—was used on

Table 14. *Comparison of trap-catches on the three subsections of the Scrub section*

		Total catch	Traps	Catch per trap	Males/Females *L.s.*	*Lc.*gp.	*C.e.*	*C.v.*	*Cyn.*	*L* : *C* ratio
15-20 Aug.	Scrub	216	4	7·7	–/1	6/33	41/131	–/1	1/2	40 : 173
	Bleatarn	912	4	32·6	–/2	62/248	197/393	2/8	–	312 : 600
11-13 Sept.	Scrub	118	8	4·9	–	4/48	7/48	1/4	4/2	52 : 60
	Gorse	137	4	11·4	–	2/26	14/80	1/11	1/2	28 : 106
15-19 Sept.	Scrub	259	8	10·8	–/2	2/38	38/159	–/10	1/9	42 : 207
	Gorse	122	4	10·2	–	1/14	14/71	–/10	5/7	15 : 95

five occasions during the July period to sample a birch bush at the edge of the small wood clearing which formed the location sampled by the four tents. The tree was about 10 ft high, and some 6 ft in diameter at the widest part of the bush. The total number of square metres trapped per subsection, and the species caught, are given in Table 13. The total catch per m^2 was higher in the Gorse than in the adjacent Scrub subsection and in the Wood than in the Lab. subsection; yet the highest rate per square metre was obtained on open-ground-formation permanent pasture. The four Wood-subsection tents on low-field-layer in a clearing caught only female *Calliphora erythrocephala*, but numerous males were caught along with females in the adjacent tree. No *C. vomitoria* were caught except in the tree, where both sexes occurred.

In the August 1951 experiment the eight traps in the Scrub section were on two locations, one in the Scrub subsection, the other in the Bleatarn (wood-edge formation) subsection (Fig. 1). In the September experiment the twelve traps were in three locations, two on the Scrub, the third on the Gorse subsection. The pooled catches during the first seven days for the first experiment, and for the first to third, and fifth to ninth days in the second experiment are given in Table 14.

The interesting feature of the August results is the startling difference in catch between the Bleatarn traps and those on the Scrub subsection, less than 100 yd away. The $L : C$ ratio and the sex-ratios of both *C. erythrocephala* and the *caesar* group are higher in the wood-dominated traps. The few *C. vomitoria* caught were almost entirely on Bleatarn. The September results showed an at present inexplicable increase of the *C. erythrocephala* catch within a matter of days on all three sections (Table 12). Equally inexplicably no increase occurred on one location on the Gorse subsection. These features serve to underline two important points. First, the mean trap catch on the Gorse for the first period is significantly greater than that on the Scrub, calculated on the assumption that location variance for low means is as stated for subsections. The difference disappears in the next

Fig. 1. Sketch of (a) the Scrub section and (b) the Lab. section, to the same scale. Trapped subsections enclosed by interrupted lines: a, the small Bleatarn portion (left, the triangular close subsection and the Scrub proper (right), with roadways between; b, the Wood (right, mostly Lab. block below the normal Fields subsection, and the hedgerows top and right. The ringed numbers are the serial trapping sites (1, Met. site; 2, W.T.; 3, G.H.; 4, Bee; 5, Wood).

few days, as does the difference in $L : C$ ratio. The change is almost entirely due to an increase of *C. erythrocephala* on the Scrub. Since the total catch and the catch of this species have not altered appreciably on the Gorse, this increase would legitimately be assumed to represent a sudden local emergence on the Scrub, were there no evidence available from other subsections and indeed examination of the individual results shows that the *C. erythrocephala* catch on one of the two Scrub locations increased sevenfold whilst the other, about fifty yards away, doubled. As it happens, there are simultaneous results from other areas, and these show a general increase of the catch of this species. On the four locations on the Lab. section it increased by 700, 400, 200 and 150%. It is thus the Gorse catch for the second period in Table 14, and not the Scrub catch, which deviates from the norm. The example effectively illustrates the need for collateral evidence to establish which condition is the control, in field comparisons.

Secondly, the sudden increase of *C. erythrocephala* on the Scrub and Lab. sections was paralleled on Moulin's, where a 900% increase occurred. The increase

may have been merely in response of the population to the bait, but if so it is surprising that, except on Modlin's, the responsible factor, weather element, quality of bait or whatever it was, did not affect the other blowfly species. Whether it represents an increase in activity or in numbers, the result emphasizes the essential instability in time of any pattern of apparent numbers, the non-universality of pattern changes, and the consequent unreliability of bait-trap comparisons unless based on results obtained over a period of time.

Bearing in mind this last caveat we may now examine the results from the massive trappings in October 1953. The catches were mainly *C. erythrocephala*, other species being poorly represented, but the results are of interest as a numerically reliable comparison of the subsections of three sections for a point in time. The eighty-four traps on each section were distributed in sets of six, each set being usually confined to a single subsection. Modlin's, which at the time of test carried a uniform cover of aftermath grass, was regarded as a single subsection. The spatial relation to each other, and the vegetation structure of the subsections

Table 15. *Comparison of October 1953 trap-catches by subsections*

	Number of traps	Total flies per trap	Catch per trap and % of total in parentheses		
			Lucilia	*C. vomitoria*	*Cynomyia*
LAB. SECTION					
Wood	15	34·5	0·4 (1·16)	0·66 (1·93)	–
Lab.	30	48·3	0·63 (1·31)	0·63 (1·31)	0·1 (0·22)
Hedgerows	24	72·4	0·38 (0·52)	0·88 (1·22)	0·08 (0·11)
Fields	15	46·7	0·92 (1·99)	0·2 (0·43)	0·6 (1·3)
SCRUB SECTION					
Scrub	60	40·3	0·63 (1·57)	0·45 (1·12)	0·39 (0·96)
Gorse	12	76	1·5 (2·22)	1·2 (1·6)	0·63 (0·84)
Bleatarn	12	28·6	0·6 (2·03)	0·75 (2·61)	<·1 (0·3)
MODLIN'S SECTION	84	36·3	1·57 (4·33)	0·38 (1·05)	0·24 (0·66)

in the Lab. and Scrub sections, are illustrated diagrammatically in Fig. 1. The catches and species-composition for the subsections are given in Table 15.

In the Lab. section the Hedgerows subsection has a significantly higher Calliphorine population than any of the others (Hedgerow—Lab. difference = 24 ± 9·3): the other three do not differ significantly from each other. In the Scrub section the three subsections radiate from a common base and at their furthest point the two outers are little over 100 yd apart. Yet the central Gorse subsection, separated only by a road from the Scrub subsection, and by a road and some 20 yd of intervening bare grassland from Bleatarn, had a significantly higher population than either, the lesser difference, 35·7, having a standard error of only ± 11·8. The Scrub-Bleatarn difference is slightly over the 5% probability limit, the difference being 11·7 ± 6·75. The Gorse subsection had a drier, more loamy soil than the peaty or acid soil of the Scrub, and it is possible that the difference may have been associated with a richer soil fauna, but this cannot account for the lack of difference in 1951 before the stands of gorse had suffered from fire, and also

fails to explain the difference between the Gorse and Bleatarn, which has a similar soil.

It is to be noted that, as with Bleatarn, the wood-associated population of the Lab. section appears to be lower than that of the Lab. or Fields subsections. In the late-season serial trappings, the trap site in the Wood also gave a lower catch than the Res. site on the Lab. subsection. Points of interest in Table 15 are: first, the *Lucilia* catch was greater, both in actual numbers and proportionately to the total catch, in the fields than on the Lab. subsection. In the Scrub section this species group are also more numerous absolutely and relatively in the Gorse than the Scrub. In 1951 the difference was negligible. Between 1951 and 1953 much of the tall-field-layer in the Gorse had disappeared. Secondly, *Calliphora vomitoria*, although absolutely most numerous in the Gorse subsection, was relatively most numerous in the wood-edge type subsection; *Cynomyia mortuorum*, on the other hand, was commoner in the most open subsection of both sections, the Fields and the Gorse. It will be noted that the pattern for the uniform aftermath on Modlin's section corresponds to the above, namely a relatively high *Lucilia* and *Cynomyia*, and a relatively low *Calliphora vomitoria* population, in open terrain with low field-layer.

DISCUSSION

The numerical assessment of blowflies in relation to the various elements of their natural environment must be approached through a study of their distribution in different biocoenoses; the biocoenose being tested for significance of association must be the whole of, and no more than, that complex included in the area for which the blowfly population is being assessed; i.e. the measurement of the blowfly component requires a foreknowledge of its spatial restrictions. Clearly, a knowledge of the spatial pattern of the distribution of flies in a community must first be gained; the nature of the observed groupings must also be known. A stable pattern suggests that the causal association is with sessile elements. The more permanent of such associations are likely to be with the physiographic factors or the structurally permanent vegetation elements, impermanent stable patterns to be associated with elements subject to aspect change, or to periodic migration. On the other hand a rapidly changing pattern showing not only changes in overall density but redistribution of the aggregations would point to the significance of the more mobile animal or the transient vegetational elements of the community.

Interpretation of the nature of the distribution pattern of fly populations requires an understanding of the mobility of the flies, since individual dispersal at random will largely determine the degree of interspersion between aggregations. As already pointed out, knowledge of dispersal patterns from concentration foci is of importance for the calculation of release-recapture estimates of population density. Equally it is obvious that the extent of 'interspersive redistribution' (the selective effect of the community on redistribution arising simply from random dispersal) must be allowed for in assessing the zone of influence of the

bait-traps, since this zone is the unit of area to be related to the estimate of population. If the distribution of the population is to be compared with that of various environmental combinations and the movements of individuals are to be studied in relation to this distribution, it follows that the population must be envisaged in terms of density, space and time. As a working concept any area in which flies tend to loiter is imagined as an 'arena of activity'. The arenas will differ in the degree of concentration within them of 'centres of action', the minor habitats of Elton (1949), which are not defined at this stage and may belong to any category of environmental factor. The attraction of flies to these and the kineses of flies as they wander at random are imagined to result in variations in the population-density of arenas according to the concentration of minor habitats, although the individual is not by definition confined to the arena, and individual emigration and immigration may be occurring, freely or rarely, at the boundaries.

The present paper is essentially a study of the numbers and species-pattern of blowflies coming at different seasons to carrion-baited traps placed in situations which could be classified in terms of their vegetational structure. For purpose of discussion let us for the present assume that the trapped flies originated in the habitat in which they were trapped. The blowfly population of the Crosby area, as seen in trapped samples, consists mainly of *C. erythrocephala*, usually representing 50 to 90%, and the '*caesar* group' which may total up to 50% or so. The two numerically important species of the *caesar* group, *Lucilia caesar* and *L. illustris*, differ from each other in habitat preference, and have a shorter activity season than *Calliphora erythrocephala*. Therefore, changes in the numbers of *C. erythrocephala* caught will always profoundly affect the population picture. Variation in catches of either of the *Lucilia* species will have a significant effect on the total only at those times when it is in relatively high numbers.

Fairly widely separated parts of the Crosby area, the experimental sections, showed significant differences in total numbers of trapped flies and also differences in species-pattern and sex-ratio. An aggregated pattern was observed for the Australian blowfly, *L. cuprina*, also (Gilmour, Waterhouse & McIntyre 1946). This could not be accounted for by chance variation or by trap differences, and the authors assumed it to be due to local variations in population density.

More surprisingly subsection units of the Crosby sections showed differences between themselves of the same nature, and the same order of magnitude, as those found between sections. The inference is that the fly population is not uniformly distributed, and that differences in density may occur between quite small, and sometimes adjacent, mosaic fragments of the vegetational habitat. A similar phenomenon was reported for *Drosophila* by Dobzhansky and Pavan (1950) who found that baits only a dozen or so metres apart attracted significantly different numbers and species-patterns. It is not surprising that a density mosaic of organisms would tend to result from the existence of a mosaic pattern of edaphic or food conditions. Thus Audy (1947, 1949) has related the patchy distribution of scrub mites to the food, moisture and vegetational conditions of the habitat. What does seem surprising is that with mobile strong-flying diptera local aggrega-

tions would be revealed by the bait-trap method. One would expect that the environmental forces responsible for a population peak at point A, as opposed to merely average density at B only some 50 yd or less away, would have failed to maintain this grouping when the strong attraction of carrion-bait was added in equal measure to the existing centres of action in the A and B arenas. A further possibility, which cannot at this stage be examined, is that the groupings are independent of the mosaic fragments, and correspond to the more or less ephemeral aggregations in ecologically uniform terrain demonstrated statistically by MacLeod (1956).

To a certain extent the vegetational character of the subsections imposed a degree of uniformity of habitat-structure, although occasionally, e.g. on the Scrub, the physical structure of the vegetation varied quite considerably within the subsection. The observed associations, causal or coincidental, might therefore be with the vegetational units or with the habitat-structure. In terms of habitat-structure, the nature of the association is by no means clear-cut. Thus, in the *caesar* group, the Bleatarn wood-edge formation had higher trap catches than those on the Scrub or Gorse tall-field-layer formations. Also the male : female ratio was less unbalanced. The Scrub section as a whole had higher *caesar* group catches than were obtained in the open-ground-formation Beanlands section. The Lab. section catches, and male : female ratio, were higher than on the Scrub, which in turn was higher than Modlin's. Yet the Lab. section had subsections representing a wide range from wood to open-ground formation, whereas the Scrub had a more restricted range from tall-field-layer to wood-edge. The serial trap results suggest that this species group is in greatest abundance in tall-field-layer with some high canopy, e.g. the G.R. site, lower in wood and lowest in open-ground-formation. Holdaway (1933) has shown that *Lucilia caesar* (including *L. illustris*?) and *L. ampullacea* prefer shade haunts, but Morison's (1937) results, which indicate fewer of the *caesar* group in his wood trap than in any of the others, suggest that this does not necessarily imply dense canopy layer.

The late-season results (October 1953) give a different picture to that for the earlier months. The open-ground Modlin's section had more *Lucilia* than the other sections, the now relatively bare Gorse subsection had more than the Bleatarn or Scrub subsections, and the open fields of the Lab. section had more than the Lab. or Wood subsections. This may be a seasonal shift of the rapidly disappearing *caesar* group population into the open, but the numbers involved were so low that no firm conclusion can be drawn. The degree of association of this group with definite structure type is probably obscured by the differences between the species; *L. ampullacea* is apparently confined to Scrub or wood formations, and *L. illustris* was trapped in much greater relative numbers under open conditions than was *L. caesar*.

With *Calliphora erythrocephala* the picture is slightly clearer. The serial trap-results (which may be regarded as a smoothed value with lower sampling error than short-term or one-day comparisons) showed a higher frequency of this species in the simpler hedge-complex (W.T. site) than in the 'hedge with canopy'

site (G.R.) or in the wood. In the August comparison there was a much higher catch and male : female ratio in the wood-edge formation of Bleatarn than in tall-field-layer (the Scrub subsection) but this exceptional catch order was reversed in the October comparison. In both the September and October tests the heterogeneous Lab. section had a higher catch, and the open-ground Modlin's a lower, than that of the Scrub section. These higher Lab. section catches also were associated with higher sex ratios. On the Lab. section, the hedgerows had higher catches than the other subsection, the Wood having actually the lowest catch, though the difference is not statistically significant.

The apparent population-level of *C. erythrocephala* may change abruptly; in the September test the catches showed up to ninefold increase within a week. As pointed out earlier, change of numbers of this numerically predominant species will profoundly affect the general picture, even though the other species do not show corresponding change; in the experiment in question it altered the ranking order of the sections. In the October test the total catch, representing almost entirely *C. erythrocephala*, showed day-to-day variations in ranking order between sections, and the evidence suggests that the actual population-level altered to differing extents. The rapid and reversible changes in relative level between sections indicates that at least one of the significant factors affecting the relative distribution of this species is able to vary independently of the section characters, and with a periodicity almost diurnal in its brevity. The main macroclimatic elements appear to be ruled out as possible causes, though the effect could conceivably be related to ecoclimate. Possibly more plausible explanations are independent and erratic emergence peaks on the sections, or even unnoted movements of the local mammalian or avian fauna. The significant changes induced by the operation of this unknown will obviously make it difficult to demonstrate with any certainty an association of the species with habitat-structure. Yet, apart from the anomalous result from the Bleatarn wood-edge subsection, the picture presented is one of reasonably consistent preference for interrupted tall-field-layer or scrub-edge habitat. In view, however, of the apparent preference of the males for canopy cover in all the bait-trap results, and of the apparent existence of an unknown but powerful association independent of habitat-structure, the above picture must be accepted with caution.

The association of numbers with habitat-structure appears to be more pronounced in the case of the less frequent species, notably *C. vomitoria, Lucilia ampullacea* and *L. sericata*, than with the major-component species. This, if proved, would be an important ecological point, but the evidence for these infrequent species is still too limited to be more than suggestive.

The anomalous results with the *caesar* group and with *Calliphora erythrocephala* may correctly reflect a low degree of correlation between the local groupings of the blowfly population and the vegetational cover or structure, the suitability of activity-arenas being determined mainly by other factors. On the other hand they may be due to the association being obscured from various causes. Three of these may be briefly mentioned here. Firstly, seasonal change of activity

arena may occur, associated possibly with such phenomena as the slowing up of physiological activity in woody vegetation, a seasonal shift of relative density of carrion, or changes in light intensity. Secondly, trap catches may not represent the population of the immediate neighbourhood only, so that differences may be levelled out by flies drawn from diversified distant areas. Thirdly, the catches, though representing the local population, may not be representative of its species proportions, because of possible interaction of time on species in their response to bait. The first, as already suggested, may be in part responsible for the irregular results with the *caesar* group. Some evidence bearing on the second cause is afforded by the tent-trap results. The Wood, even apart from the tree-tent catches, yielded a higher catch of *C. erythrocephala* per m^2 than did the remainder of the Lab. section. Yet the highest catch obtained, and the greatest number of males, were on an open-ground permanent pasture, the nearest equivalent to which on the Lab. section was the 'open fields' subsection. This suggestion of a lack of constant association with vegetation structure, even with unbiased samplings, is interesting, but obviously much more intensive tent-trapping evidence is required. The third cause is the justification for the release-recapture experiments. Those described in this paper are of comparative value for *C. erythrocephala* only, and until adequate results are available, the possibility of this cause being operative must remain.

To sum up: the evidence presented in this paper suggests that there is some degree of association between fly-numbers and structurally classified vegetation-habitats. The relative significance of the different habitats appears to be inconstant, and differences in population-level apparently occur which cannot be explained in terms of habitat-structure. Remaining approaches are to attempt to relate the observed groupings to the floral composition of the ground-cover, to physiographic differences, to carrion distribution, and to ecoclimate. The difficulties of interpretation in the work described here indicate the desirability of a much more detailed knowledge of the dynamics of the fly population itself, as an antecedent to these approaches. The nature of population aggregations and the causes underlying their development and dissipation, the problem of changes in population numbers and species-pattern and the related problems of individual dispersal and population interspersion, are at present being severally examined, and will be discussed in later papers.

SUMMARY

1. The relation of blowfly populations to season and to vegetational environment was studied over a number of years by serial trappings on the periphery of an aerodrome in a mixed-farming area near Carlisle.

2. Throughout the blowfly season the population consisted mainly of *Calliphora erythrocephala*, and this species was the first to appear and the last to disappear. The *Lucilia caesar* group formed a second major component in the summer months, representing up to 40% of the total. Within this group, *L. illustris* was slightly more frequent than *L. caesar* and *L. ampullacea* relatively scarce. *Lucilia*

sericata and *L. silvarum*, *Phormia terrae-novae* and *Cynomyia mortuorum* were all present in low numbers only; *Calliphora vomitoria* occasionally represented up to 10% in the late season. Other species of Calliphorine blowflies were only rarely caught. Differences between species occurred in the sex-ratio of the trapped samples, and these varied between seasons and for different types of habitat.

3. A species-pattern similar to the above was obtained on reclaimed bogland and on upland sheep-grazing.

4. The general proportions of the major species-groups in the population were confirmed by tent-trapping of the ground without attractant bait.

5. Differences in total catch and in species-pattern between the five different vegetational habitats sampled are analysed in relation to season.

6. *Calliphora vomitoria* and *Lucilia ampullacea* apparently need dense cover such as wood. *Calliphora erythrocephala* was more numerous in the open near hedgerows than in wood, *Lucilia caesar* preferred tall-field-layer with some interrupted canopy, and *L. illustris* rather more open conditions. There is possibly a shift of some species of the *caesar* group population into more open conditions in the late part of the season. Relatively more males of *Calliphora* and *Lucilia* were caught by bait-traps in canopy habitats than elsewhere; this was not confirmed by the tent-trap catches.

7. The populations on different sections of the area in August, September and October were examined by intensive bait-trapping and by marking flies and releasing them again.

8. *Calliphora erythrocephala* was estimated at 50 to 200 flies per acre in August, 400 to 1000 in September, and 700 to 1000 in October. The *caesar* group was estimated as 40 to 70 per acre in August and September, and under 1 per acre (*Lucilia caesar*) in October. *Lucilia sericata* and *Cynomyia mortuorum* were estimated to be in very low numbers.

9. Bait-trap estimates of relative numbers showed significant differences in total blowfly population between the sections. The relative order of population-density of sections may change between tests, and sometimes within a few days during a single test. This latter effect is apparently due to the *Calliphora erythrocephala* component.

10. Bait-trap estimates of the population of ecologically uniform subsections of each section showed significant differences in population level and also differences in species-pattern. The relative level of population in different vegetational types varied between tests, and in the case of *C. erythrocephala* even within a few days. The apparent preferred habitats of the different species in the subsection tests were as found in the serial trap results, and the males of *C. erythrocephala* and the *caesar* group similarly were relatively more numerous in canopy cover.

11. The concept of arenas of activity as applied to blowflies is outlined in general terms.

12. Some limitations to the use of the release-recapture method of estimating numbers are discussed in relation to the results.

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THE BREEDING, GROWTH AND AGE STRUCTURE OF A POPULATION OF THE LEECH *HELOBDELLA STAGNALIS* (L.)

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(With 3 Figures in the Text)

The population studied spends the summer months on the leaves of a bed of *Acorus calamus* L. in Whiteknights Lake, Reading, Berkshire. When the plants die down in autumn the leeches aggregate among the roots and on the under sides of the rhizomes. They migrate upward again as the leaves develop in spring, and soon after this the leaves become densely clothed with chironomid (tendipedid) larvae. These appear to form the staple diet of the leeches, which use their proboscides to suck the body fluids, haemoglobin from which may often be seen by transparency in the gut of the leeches. It has been shown (Mann 1955) that *Helobdella* occurs most abundantly in hard, eutrophic lakes and ponds, and that it colonizes reed beds in preference to stones. Whiteknights Lake has about 90 p.p.m. of calcium, so the leeches on the *Acorus* are living in something approaching their optimum habitat, and the life cycle observed is probably fairly typical.

Samples were collected from April to September by breaking off shoots of *Acorus* at their junction with the rhizome and continuing the process until 50-100 leeches had been obtained. A note was kept of the number of shoots examined, so that the density of the population could be expressed in terms of leeches per shoot. In the autumn the shoots died down, and no comparable estimate of density could be made. The winter samples were obtained by pulling up the rhizomes and searching among the adventitious roots, but this destructive operation was carried out as seldom as possible. In the autumn of 1953 samples were collected from several different lakes. The leeches were dried on filter paper, weighed to the nearest 0·1 mg on an air damped direct-reading balance, and their weights were grouped in 1 mg classes. The frequency polygons obtained were found to be similar in shape for samples from different lakes, and for samples from different reed beds within the same lake. The *Acorus* bed in Whiteknights was chosen for the full study, and regular samples were taken from December 1953 to November 1954. At the end of that time it was found that the shape of the frequency polygon obtained was not the same as that obtained in the previous autumn, so the sampling was continued for another year.

Helobdella lays its eggs in a thin, transparent cocoon which it then fastens to the ventral surface of the body (Brandes 1886-1901). The embryos on hatching become attached to the ventral surface of the parent, and are carried about for

a few weeks. It was found that in April most of the leeches were carrying cocoons, in May most were carrying young, and in June the young had been liberated and the parents had died. The April sample in each year was killed in alcohol and the eggs removed from the parents and counted. All other samples were returned alive to the lake.

Fig. 1 shows the weight-frequency distribution of ten samples taken between December 1953 and November 1954 together with a selection of the samples of 1955. In April the over-wintering population of 1953-54, labelled A_1, is made up principally of leeches carrying eggs. In May the same population is carrying young, but by June the adults form well under one-third of the sample, the remainder being small leeches, B_1, which are clearly the offspring of the A_1 group. By July 72% of B_1 are breeding, and A_1 is represented by only one leech. In August A_1 has disappeared, B_1 is represented by breeders and non-breeders in almost equal numbers, and a new element, C_1, has appeared, which represents the offspring of B_1, resulting from the egg-laying in July. The samples in September, October and November show a population made up of about one-third B_1 and two-thirds C_1, and this is the over-wintering population. The November 1954 polygon does not correspond in shape with that for December 1953. The similarity of the polygons for September, October and November 1954 shows that the difference between the two years is not due to a sampling error, especially as the 1953 type of polygon was obtained several times from different habitats. Accordingly, the sampling was continued for another year.

All the important changes in population structure in 1955 occurred between May and September, so only these months are displayed in Fig. 1. In May 70% of the population is breeding, but if this fact is ignored and a single polygon is constructed for the whole population (see dotted line) it is seen that the shape is the same as those obtained in the previous autumn. The only change is an increase in the weight recorded for the breeding specimens, due in part to the extra water carried over when weighing complete with brood. If we call the May population A_2, then the new element present in June, B_2, is clearly the offspring of A_2. The July sample is made up entirely of B_2, and 61% are breeding. Since there is almost no breeding activity in August it appears that about one-third of B_2 failed to reach maturity in 1955. In August the offspring of B_2 appear as a new peak, C_2, and there are two peaks in the B_2 population, B_{2a} and B_{2b}. B_{2a} persists in September, and (although not illustrated) into October and November, as part of the over-wintering population, while B_{2b} disappears before September (and in August probably consisted of leeches which had produced a brood, lost it, and were about to die). The B_{2a} leeches are probably those which failed to reach maturity in 1955 and are deferring breeding until the following spring.

The frequency polygon for September 1955 now corresponds with that for December 1953. The difference between the two years studied is in the relative proportions of B and C broods present in the over-wintering population. This is probably dependent on the proportion of the B leeches which reach maturity in the summer in which they were born. If the proportion is high, then most die

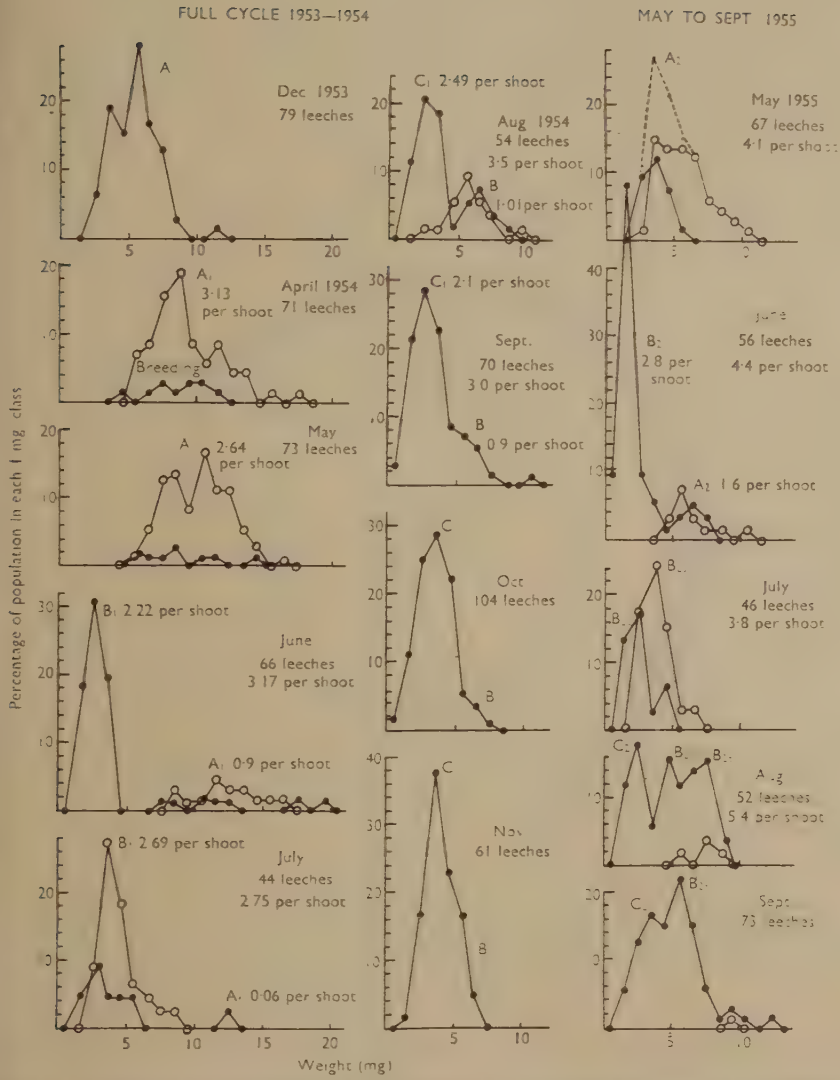

Fig. 1. Frequency polygons representing the distribution of the weights of leeches in 1 mg classes in 10 samples taken between December 1953 and November 1954, and in certain of the samples taken between December 1954 and November 1955. Numbers of breeding leeches are recorded separately as open circles.

after breeding, and few survive the autumn, and the over-wintering population is made up predominantly of the C brood, i.e. the summer brood. If, on the other hand, a smaller number of the spring brood reach maturity before the winter, a large proportion survive alongside the autumn brood. This happened in the autumn of 1953 and 1955.

The density figures, in terms of leeches per shoot of *Acorus*, are also given in Fig. 1 for those months where the shoots were well grown. The decline in the A_1 population from April to July 1954, following breeding, is shown by the fall from

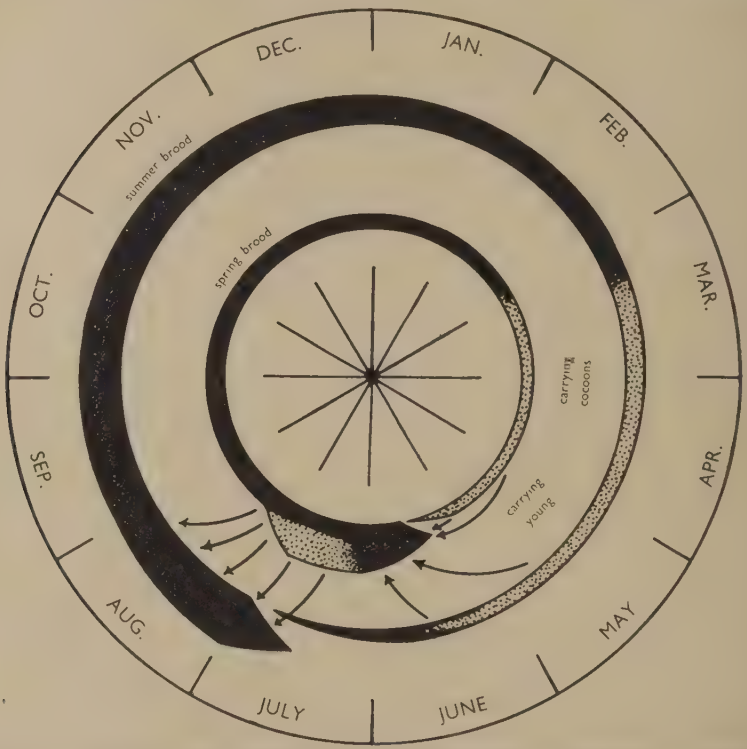

Fig. 2. Diagram illustrating the cycle of events observed in 1953-54 and 1954-55. The width of the line is roughly proportional to the density of the population. Dotted areas indicate breeding leeches. Arrows indicate the release of young by the parents.

3·13 to 0·06 per shoot. The greatest density recorded for the B_1 population is 2·69 per shoot in July, and this falls to 0·9 per shoot in September. Similar trends are shown by the figures for 1955.

The mean number of eggs carried was 17·2 per leech in April 1954 and 13·5 per leech in April 1955. In 1955 the leeches were weighed before and after the removal of the eggs, and when the weight of the eggs was expressed as a percentage of the weight of each parent, the average figure was 13·4% with extremes of 8·4% and 16·7%. Assuming that this figure is applicable to other breeding periods, it is

important in confirming the interpretation of the change in the samples between July and August 1954. It might be argued that C_1 in August represents the leeches in B_1 which were breeding in July, and which showed a fall in mean weight as a result of losing the brood. The mean weight of B_1 in July is about 4 mg and the mean weight of C_1 in August is less than 3 mg, so for this hypothesis to be true, the weight of the brood would have to be over 25% of the weight of the parent plus brood. This was not the case.

DISCUSSION

The life cycle of *Helobdella stagnalis* differs markedly from those of *Erpobdella octoculata* and *Glossiphonia complanata* (Mann 1953, 1957) because few, if any, individuals of *Helobdella* live for more than one year, and many die after only three months of life, while most leeches of the other two species live for two years, if they survive the initial period of high mortality. The annual cycle of events for *Helobdella* has been summarized in Fig. 2. The over-wintering population consists partly of leeches hatched in the previous May or June, and partly of those hatched in July or August, the relative proportions of these two components varying from year to year. In April and May both of these groups breed, and their offspring are first seen in the samples in June. The over-wintering population now dies off, and the spring brood themselves begin to breed in July, their offspring appearing in the samples in August and September. A proportion of the spring brood, probably those leeches which do not breed in July, live through the winter alongside the August-September brood.

The mortality at different times of the year may be calculated from the density of the breeding leeches and the density of their offspring. In April 1954 the breeding population was 3·13 per shoot, and each carried an average of 17·2 eggs so that if all had hatched and the young had all survived until June, the density of the offspring would have been 53·8 per shoot. The highest observed density was 2·69 per shoot, in July, and this suggests a mortality of 95% between April and July. The July population suffers a decline of 62% by August, and the density in September is 10% below that of August. A hypothetical population of 1000 newly hatched young in April would be reduced to 50 by July, to 17 by August, and to 15 by September. In April 1955 the density on the *Acorus* was greater than in 1954, but the number of eggs carried by each was smaller, so that the potential density of the offspring was about the same, 55·3 per shoot. The mortality in the month following breeding was less severe, only 5·25%. This fits in very well with the suggestion that in 1955, as in 1953, fewer leeches bred in the summer, and more survived the winter to breed in the spring.

The pattern of survival for *Helobdella* is very like those worked out for *Erpobdella* and *Glossiphonia*, except that the time scale is different. In each case more than 90% of the offspring are lost early in life, but those surviving this initial critical period have a relatively high expectation of life. Owing to the decay of the shoots in autumn, it was not possible to follow changes in population density of the summer brood.

By noting the mean weight of each group, A, B and C at different times of the year, it is possible to deduce the approximate rates of growth. In Fig. 3 growth curves for the two broods of 1954 have been plotted alongside those for *Glossiphonia complanata* of the same year in a different habitat. During the summer months the rates of growth of the two species are comparable, but the greater size of *Glossiphonia* at one year of age is due to its continued growth through the autumn and early winter, when *Helobdella* almost stops growing. Related to the small size of breeding specimens of *Helobdella* is the smaller number of eggs produced, 13 to 17 compared with about 33 for *Glossiphonia* and 23 for

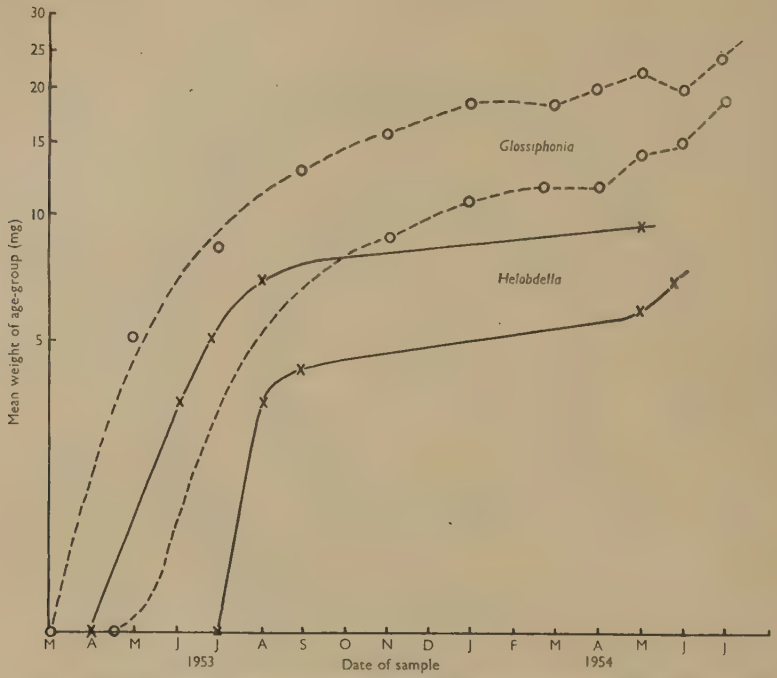

Fig. 3. The curves of $\log n + 1$, where n = mean weight of population in mg, plotted against time for two broods of *Glossiphonia* from the River Pang (Mann 1956) and two broods of *Helobdella* from Whiteknights Lake.

Erpobdella. This would place the species at a serious numerical disadvantage in the face of the observed mortality if it were not for the second generation produced in the summer. This brings the figure for the possible offspring of a single parent in one season to something well over 100, and accounts for the fact that *Helobdella* is usually the most numerous leech in eutrophic lakes (Mann 1955).

It thus appears that *Helobdella* is adapted to making the most of a short season for growth and reproduction, reaching maturity at a smaller size, and much earlier in life than *Glossiphonia*, and producing smaller broods more often. The rhythm of life is closely linked with the annual cycle of growth and decay of the plants on

which it lives, and is made possible by the large number of potential food organisms which colonize these plants. The chironomids (tendipedids) present are mostly leaf-mining filter feeders which utilize the plankton and suspended detritus of the lake water (Walshe 1951), and it is probable that these find their optimum habitat in eutrophic lakes where there is normally an abundance of this type of food. The exact role of the chironomids in the *Acorus* community is a subject for further investigation.

ACKNOWLEDGMENT

I wish to thank Professor A. Graham for his interest in the work and criticism of the paper.

SUMMARY

1. The life history of the leech *Helobdella stagnalis* was investigated by taking regular samples from a population on a bed of *Acorus* in an eutrophic lake. The leeches produced a brood in May, and then died. A proportion of their offspring were breeding in July and August, the remainder reproduced in the following spring. Those leeches hatched in August also reproduced in the spring.

2. Compared with *Glossiphonia complanata*, *Helobdella* has a more marked annual rhythm of rapid growth in summer and slow growth in winter. It reaches maturity at a lower body weight, and produces smaller broods more often. This annual rhythm corresponds with the annual rhythm of growth and decay of the plants on which it lives.

3. The pattern of survival is similar to that found in *Glossiphonia complanata* and *Erpobdella octoculata*, *i.e.* about 95% mortality in the first three months of life, followed by a period of much reduced mortality. The biotic potential of *Helobdella* is greater than for the other two species, and accounts for the fact that it is usually the most numerous species in eutrophic lakes.

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THE ORIENTATION OF BARNACLES TO WATER CURRENTS

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(With Plate 6 and 7 Figures in the Text)

INTRODUCTION

Investigations have shown that barnacle larvae select suitable sites in relation to (*a*) depth (Hutchins 1952), (*b*) illumination (Pomerat & Reiner 1942, McDougall 1943, Gregg 1945, Weiss 1947, Barnes, Crisp & Powell 1951), (*c*) surface contour (Crisp & Barnes 1954), and texture (Moore & Kitching 1939, Pope 1945, Gregg 1948, Pyefinch 1948, 1950), (*d*) the presence of previously settled individuals of the same species (Knight-Jones & Stevenson 1950, Knight-Jones 1953), or of related species (Knight-Jones 1955) and (*e*) the velocity gradient of currents at the surface of the substratum (Crisp 1955). If the current flow relative to the substratum is too great, the cyprids fail to attach (Smith 1946, Korringa 1948). In addition to selecting a particular site, they orientate at settlement to surface contour and light (Barnes, Crisp & Powell 1951) and possibly also to water movement (Crisp 1955). Orientation along grooves (rugotropism) has been investigated by Crisp & Barnes (1954) who showed that it was a sensitive reaction invoked by contact with irregularities in the surface. Rugotropism was shown to override other orientation responses.

In spite of statements to the contrary by Visscher (1928) the conclusion that cypris larvae orientate positively to light at settlement appears inescapable. Hiro (1939), McDougall (1943), and Pyefinch (1948) all recorded positive responses, and Barnes, Crisp & Powell (1951) showed a positive orientation to light in *Balanus balanoides* and *B. crenatus* while in *Elminius modestus* the proportion of individuals orientating towards the light could be correlated with the proportion of illumination falling in a given sector. They suggested that orientation to light might possibly have survival value since it would bring the eyes of the adult into the direct path of the incident light; nevertheless they thought it probable that this reaction might be non-functional, a continuation of the positive reaction to light shown throughout the planktonic phase. Knight-Jones & Crisp (1953) made observations of cypris larvae of *B. balanoides* during the setting process

and recognized that response to contour and to light were distinct reactions taking place just before fixation; they were not in evidence during the exploratory crawling phase.

Orientation to water currents is less firmly established. Moore (1933) made measurements of the orientation of young and older individuals of *B. balanoides*, and interpreted the difference which he found as being due to a rotation of the shell during growth. Later (1935) he suggested that the spiral pattern of the basal canals in *B. improvisus* was due to rotation during growth. He believed that the cypris would at first be orientated passively by water currents, so that its anterior end faced upstream, but that later, by rotation through 90°, it would come to lie across the water current. It could then fish with equal ease—or discomfort—in ebb or flood currents by twisting the cirral net through 90°. Hiro (1939) and McDougall (1943) both adduced evidence to show that even in a current cyprids orientated with the anterior end towards the light. Hiro apparently believed that orientation to current could occur but had little evidence to support it.

Barnes, Crisp & Powell (1951) criticized Moore's conclusions on the grounds that all the evidence pointed to the preponderance of light over water currents in causing the initial orientation of the cypris and drew attention to a tendency for barnacles to orientate towards the edge of a panel. They also showed that for many species growing under normal conditions in the sea no change in orientation could be traced from serial photographs. Crisp (1953), however, showed that in certain species with canals in the basis, a change in orientation of the shell often accompanied growth, and confirmed Moore's (1935) view that the direction of rotation corresponded with that of the twist of the basal canals. This rotation enabled the cirral net to beat more directly into the current. Crisp (1953) believed that rotation was due to differential growth at the base, caused by the torque exerted by the animal during feeding, when the cirri were twisted to face the current. He also brought forward evidence (Crisp 1955) that in the absence of other stimuli the cypris larva showed a weak orientation at the time of settlement with the posterior end upstream, i.e. in the opposite sense from that postulated by Moore.

In this paper we shall consider how water currents influence the orientation of those species of barnacle which have hitherto been considered to show negligible rotation after settlement (Barnes, Crisp & Powell 1951), namely *B. balanoides* (Linn.), *B. crenatus* Brug. and *Elminius modestus* Darwin.

ORIENTATION OF THE ADULT TO CURRENT

Barnacles are not usually exposed to unidirectional currents, so that the influence of current, unlike that of light, is not readily demonstrated under natural conditions. If, however, a craft is moored from one end in a tideway its surface will be exposed to currents of varying intensity but in a constant direction. On the sides of the craft there is normally a gradient of illumination, which causes a

strong orientation of the cyprids, but on the under surfaces the light gradient is much weaker. It would clearly be minimal on the underside of flat-bottomed craft moored in very turbid water. A clear example of the orientation of adult barnacles was observed on the underside of a flat-bottomed barge moored in the estuary of the R. Conway, North Wales. The bottom was devoid of algal growth and had received a heavy settlement of *Balanus balanoides* in the spring of 1952. Few of them had settled on the sides of the barge, which were populated

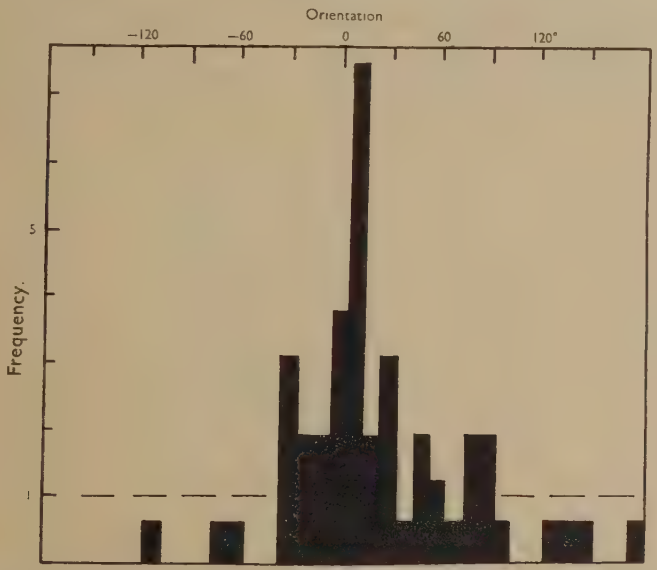

Fig. 1. Histogram of the orientation of individuals on the underside of a barge at Conway. Zero angle refers to individuals with the rostrum pointing upstream and carina downstream. Illumination is predominantly from the sectors with positive angles. Frequency is given as fraction of population per 10° sector × 36, so that unit frequency is the most probable value for a random orientation, and is shown by the dotted line.

by *B. improvisus* and *B. crenatus*. These species settle later in the season than *B. balanoides* and had presumably been excluded from the under surfaces which were already occupied. When examined on 6 August 1952 the carinal end of almost every *B. balanoides* was found to be directed towards the rear end of the barge, so that when the cirri were in the fishing position the water current flowed into the cirral net. A slight tendency for individuals to the right and left of the mid line to point outwards towards the light can be noted from the orientation diagram shown in Fig. 1.

In order to present the results in a simpler form the histogram can be resolved into vectors (Barnes, Crisp & Powell 1951). The components of orientation in the direction of the current are averaged according to the formula

$$A = 1/N. \sum_{i} \cos \Phi_i$$

where Φ_i is the angle of orientation of the ith individual, and N the total number

of individuals in the sample. The angle Φ is the angle between the rostro-carinal axis and the direction towards which the current is flowing (Fig. 2). The component at right angles to the current may similarly be resolved,

$$B = 1/N. \sum_i \sin \Phi_i.$$

The resultant vector R will equal $\sqrt{A^2+B^2}$ and the angle Θ which this makes with the current axis will be given by

$$\Theta = \tan^{-1} B/A.$$

Usually light falls in a direction approximately at right angles to that of the current. We therefore adopted the convention that deviations (Φ) from the direction of the current are to be regarded as positive towards the illuminated side. This convention is illustrated in Fig. 2.

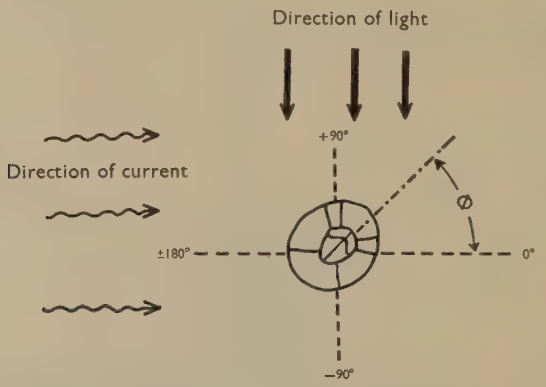

Fig. 2. Convention for measurement of orientation of barnacle to current.

The value of the components in the direction of the current ($R \cos \Theta$) and at right angles to it ($R \sin \Theta$) supply most of the information of the histogram. The maximum value for R is 1·0 when all individuals are orientated in the same direction. In Fig. 1 the value of R is 0·67 and $\Theta = 20°$; the component of the orientation in the direction of the current $R \cos \Theta = 0{\cdot}63$, indicating a strong tendency to orientate to the current. The value of $R \sin \Theta$ is 0·23, indicating a weaker orientation to light.

A number of measurements of barnacle orientation have been made under conditions of unidirectional flow and these are summarized in Table 1. The structures on which barnacle orientations were measured were of three kinds. Firstly there were submerged parts of craft of various types, which had been moored from one end. The orientations had to be measured often from awkward positions while the boats were beached, and on this account may not be very accurate. The orientation, however, is clearly significant in all cases. The most strongly orientated barnacles were found on the bottom of the flat barge moored in a narrow part of the R. Conway, and the weakest orientations on two small shallow-draughted dinghies which had been left afloat for some time in the R. Crouch.

The second group of experiments were carried out on experimental panels which could be withdrawn and measured in the laboratory. The panel exposed at the entrance to Chichester harbour was fixed to a large raft swinging with the current and was partially shaded by it. The average vector for all of the barnacles present on the front and back surfaces was 0·24. Thus the current had a small but very significant effect on orientation having regard to the numbers measured (more than 1000). The experiments in the Menai Straits were conducted on a vertical wooden board about 30 cm square, attached at one end by swivels to two lengths of chain, the upper length of chain being fixed to a floating support, and the lower chain being held in position by a heavy weight hanging from it (Fig. 3). The board

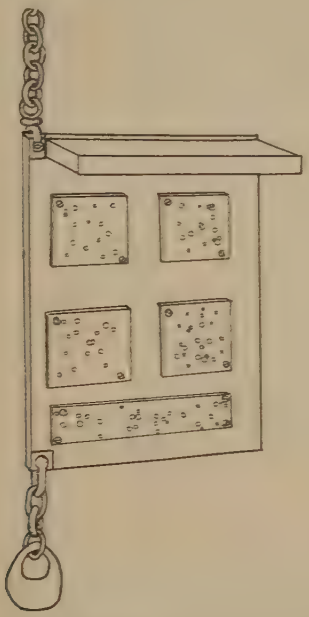

Fig. 3. Swivel device for maintaining sessile animals in a unidirectional current.

was thus maintained well below the water surface and swung with the current so that one end faced the current at all times, on the same principle as a weather-vane. Three species, *Balanus balanoides*, *B. crenatus* and *Elminius modestus* were all shown to have significant orientations produced by the current flowing over the surface of the board.

Lastly we were able to investigate two conduits which were used by industries to supply sea-water. Both conduits were enclosed and completely dark, so that the current was the only orientating influence at work. At Brighton 'A' Station, C.E.A., Southwick, Sussex, sea-water is drawn into the plant continuously through a covered concrete conduit (Crisp & Molesworth 1951). The depth of water varies

from about 60 cm at the intake end to 100-120 cm at the plant end and the rate of flow is of the order of 120 cm/sec (2·4 knots), about 15 cm from the conduit wall.

Whilst investigating the fouling in the conduit in July 1951 it was noticed that a large proportion of the barnacles on the side walls (*Balanus balanoides*) were orientated with the carinal end of the shell downstream. It was estimated that the majority were disposed in a segment 45° either side of this position. When a more detailed examination was made in September 1951 considerable numbers of *Elminius modestus* were present, also *Balanus improvisus* Darwin and *B. amphitrite* Darwin var. *denticulata* (Broch), but insufficient for the present purpose. The material measured comprised only *B. balanoides* and *Elminius modestus*. In the limited time available, 184 barnacles were measured for size and orientation. The results for larger specimens referred entirely to *Balanus balanoides* and for small ones to *Elminius modestus*. The overlap in the 8-9 mm range showed a similar orientation, but as it contained both species it is not included in Table 1.

Table 1. *Orientation of adult barnacles to water current*

			Component in direction of current
CRAFT MOORED IN TIDEWAY			
Beneath flat bottom barge, R. Conway	6 August 1952	*B. balanoides*	0·62
	2 July 1953	*E. modestus*	0·67
Sides of M.V. *Nautilus*, Menai Straits	June 1953	*B. balanoides*	0·475
Dinghies, R. Crouch		*E. modestus*	0·35
EXPERIMENTAL SURFACES HUNG FROM RAFTS, ETC.			
Steel panel suspended from raft, Chichester harbour		*E. modestus*	0·24
Swivel device, Menai Bridge, in weak current	9 June 1953	*B. balanoides*	0·32
in strong current	7 July 1953	*B. crenatus*	0·75
	26 August 1953	*E. modestus*	0·70
ARTIFICIAL CONDUITS			
Sea water conduit, Brighton		*E. modestus*	0·34
		B. balanoides	0·26

There was considerable variation in the angle adopted, but almost 70% were orientated within $\pm 90°$ of the direction of the current. In the absence of light there was no tendency for the barnacles to orientate upwards, as they generally do in illuminated sites; in fact there were more deviations in the downward direction, Θ deviating 38° from the horizontal in *Balanus balanoides* and 22·5° in *Elminius*. However, when the conduit was examined again in October 1952 a small sample of barnacles showed an orientation of the same order ($R \cos \Theta = 0{\cdot}29$) but the deviation was towards the roof of the conduit ($\Theta = -27°$).

At Amlwch, Anglesey, sea-water for bromine extraction is drawn through a large tunnel opening below low-water mark. The fauna attached to the walls was examined in March 1954. Because of periodic chlorination to reduce fouling the fauna was limited, consisting only of large tufts of *Tubularia larynx*, together with scattered individuals of *Elminius modestus*, *Balanus crenatus* and the lamellibranch *Anomia ephippium*. The majority of individuals of both *Elminius*

View of the genital aperture of a female humpback whale *Megaptera nodosa* infested by *Coronula diadema* and *Conchoderma auritum*. The posterior end of the whale is uppermost in the photograph, and the *Coronula* are almost all orientated with their carinae pointing in this direction.

(*Facing p. 185*)

modestus and *Balanus crenatus* were clearly orientated with the carinal end away from the current. There seemed to be a tendency for *Anomia* to be orientated also, most individuals lying with the hinge facing the source of the current.

It follows that the three species, *Balanus balanoides*, *B. crenatus* and *Elminius modestus*, which have not hitherto been shown to rotate during growth, nevertheless show as adults a strong orientation to current provided they have been subjected to unidirectional flow.

ORIENTATION OF BARNACLES ON WHALES

Under natural conditions the influence of the current on orientation is not noticeable since the water frequently changes its direction. The sides of a moored vessel are an artificial environment in that they change position when the current

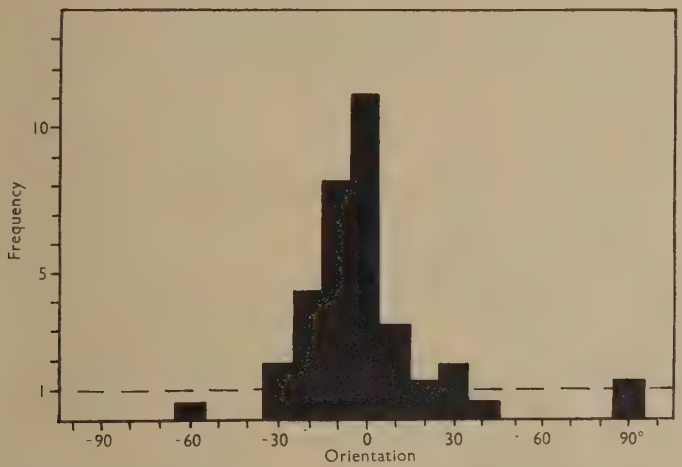

Fig. 4. Orientation of *Coronula diadema* on the ventral surface of whales. Zero angle refers to individuals with the rostrum directed towards the anterior end of the whale. The frequency scale is the same as in Fig. 1.

changes its direction. There are, however, examples of species which in their normal habitat experience unidirectional flow; namely those species which settle on the surfaces of swimming animals. The whale barnacle *Coronula diadema* (L.) settles on various species of whale in the Antarctic and is often found on the ventral surface of the whale in the vicinity of the genital aperture (Plate 6). The barnacles shown in the plate clearly have their carinal end directed towards the posterior end of the whale, so that the cirral net faces the direction of flow of water over the whale when it swims forward. Fig. 4 shows in the form of a histogram the orientations of a number of *Coronula diadema* measured in respect of the anteroposterior axis of the whale, and is based on several photographs of different whales.

THE INFLUENCE OF CURRENT AND LIGHT OPERATING SIMULTANEOUSLY

Whereas the orientation of barnacles in closed sea-water conduits approximated closely to that of the current itself, the resultant direction of orientation of barnacles growing in daylight always deviated from the current towards the direction of the prevailing illumination. This deviation varied not only from one experiment to another, but also among the different sections of the objects investigated. This variation could always be explained if the relative strength of the water flow and light gradient were taken into account, though no quantitative treatment was possible under the conditions prevailing in the sea. Table 2 gives a number of results which show how current and light together influence the resultant orientation of barnacles which are mature or approaching mature size. The table gives the component of orientation in the direction of the light, which is

Table 2. *Combined effect of water current and light gradient on orientation*

			Component in direction of light	Component in direction of current	Angular deviation of resultant from current
Flat bottom barge, R. Conway, horizontal surface		*B. balanoides*	0·23	0·63	20°
Sides of M.V. *Nautilus*, Menai Straits		*E. modestus*	0·33	0·67	26°
Sections of hull numbered from forward end:		*B. balanoides*			
1 (bow)	10° from vertical		0·57	0·31	62°
2 (forward quarters)	15-20° ,, ,,		0·32	0·29	48°
3 (amidships)	15-45° ,, ,,		0·36	0·59	31°
4 (amidships)	15-45° ,, ,,		0·37	0·54	34°
5 (after quarter)	15-40° ,, ,,		0·37	0·65	30°
6 (rudder)	vertical face		0·66	0·36	62°
Dinghies, R. Crouch:		*E. modestus*			
forward section, 45° from vertical			0·46	0·16	71°
amidships, 60-85° from vertical			0·14	0·36	21°
after section, 30-50° from vertical			0·30	0·61	26°

assumed to be vertical and at right angles to the direction of the current. It gives also the component in the direction of current and the resultant angle of orientation. The component in the direction of the light is, as would be expected, much greater on vertical or nearly vertical surfaces, and least on surfaces which are horizontal or nearly so. The component in the direction of the current varies considerably, but is in every example smaller at the forward end and greater at the after end. This tendency cannot be interpreted as an indication that the effect of current exercises more influence at the after end, for the velocity close to the hull will be greatest at the bow where the full flow of the current first strikes the boat, and least at the stern where the momentum of the water flowing past has been reduced by friction. The component of orientation in the direction of the current is greater at the after end, probably because at this end the shade produced

by the vessel influences the orientation in the same sense as the current. On the other hand, at the forward end the gradient of illumination formed by the vessel would orientate the barnacles so that their carinae pointed forward, and would therefore be opposed to the orientating influence of the current.

The angle of orientation, in so far as it is a resultant of the effects of light and current, would be expected to deviate from the direction of the current more at the forward end of the vessel than at the after end, and to deviate more on vertical parts of the hull than on those which were at an angle to the vertical or which were horizontal. Table 2 shows that this is fully borne out, even when comparisons are made between craft moored in different places.

EDGE EFFECTS

Panels were exposed in the well of an Admiralty Corrosion Committee raft in Chichester Harbour, where they were illuminated mainly from below and were

Table 3. *Influence of baffles on orientation at edges of plate*

Panel		θ	R	Component towards panel edge $-R \sin \theta$
I	Unscreened	$-18°$	0·92	$+0·28$
II	Central 8×8 in. baffle	$+8°$	0·82	$-0·11$
III	16 in. square screen with 8×8 in. central aperture	$-39°$	0·92	$+0·58$

entirely shaded from above. A settlement of *Elminius modestus* and *Balanus improvisus* occurred on these panels with a bimodal pattern of orientation. The individuals fell into two equal groups, each group deviating by an angle of approximately 55° from the right and left of the downward vertical direction. This was probably due to the light being scattered from beyond the sides of the raft and so illuminating the panels somewhat more from the sides than from below. A separate analysis of orientations of barnacles to the two edges of the panel showed that the orientation at each edge had a pattern essentially similar to that of the panel as a whole. However, there appeared also to be a slight edge effect similar to that described by Barnes, Crisp & Powell (1951). This was revealed by the presence of about twice as many individuals directed towards the nearer edges of the panel than were directed towards the more distant edge; also the resultant angle of the former diverged from the vertical slightly more than did the resultant angle of the latter.

The net orientation towards the edges of the panel might be due to light, to the effect of water flowing over the surface of the panel and passing off its edges, or to the behaviour of the larvae near the edge of the panel. Barnes, Crisp & Powell (1951) suggested an explanation based on the supposition that the larvae might settle with their carinal ends pointing in the same direction as that in which they had been walking. This explanation must now be abandoned, since direct observations show that the cypris turns frequently when exploring, especially

towards the end of its journey just before fixation (Knight-Jones & Crisp 1953).

In order to test whether the flow of water over the edges of the panel had an appreciable effect in promoting edge orientation, three 10×10 in. panels were exposed at right angles to the current so that it impinged directly on the face of each panel. Panel I was exposed unscreened. Panel II had a screen 8×8 in. in front so that the flow of water over the edge of the 10×10 in. panel behind would be prevented. Panel III was screened by a panel 16 in. square with an 8×8 in. hole in its centre to allow water to flow on to the centre of the 10×10 in. panel and spill over its edges to a greater extent than in panel I. Table 3 gives the orientations on 4×2 in. areas on the left edge of the 10×10 in. panels, Θ being measured as a deviation from the direction of the light (vertical).

Table 4. *Orientation by water current of different size-groups*

		Size-group	Component in direction of current	Angle of resultant from current
Underside of barge, Conway	*E. modestus*	>0·5 cm	0·67	26°
		<0·5 cm	0·60	30°
Swivel device, Menai Straits; strong current	*E. modestus*	>4 mm	0·43	49°
		1-4 mm	0·38	59°
		<1 mm	0·28	66°
Sides of M.V. *Nautilus*, Menai Straits	*B. balanoides*	>6 mm	0·63	37°
		<3 mm	0·35	62°
Swivel device, Menai Straits; weak current	*B. balanoides*	>6 mm	0·00	90°
		<3 mm	0·09	70°
Swivel device, Chichester Harbour	*B. balanoides*	newly metamorphosed spat	0·03	87°
		Cyprids	0·17	78°
Underside of barge, Conway	*B. balanoides*	0·7 cm mean size	0·63	20°
		0·5 cm mean size	0·70	26°
Sea water conduit	*B. balanoides*	12 mm mean size	0·23	38°
		11 mm ,,	0·38	33°
		10 mm ,,	0·22	44°
	E. modestus	7 mm ,,	0·45	31·5°
		6 mm ,,	0·36	3°
		5 mm ,,	0·21	33°

Whilst there was strong orientation to light, these figures show the effect of current in producing an 'edge effect' on orientation. In the absence of a current the resultant orientation was +8°, slightly away from the vertical panel edge. On an unscreened panel facing the current the barnacles tended to turn slightly in order to take advantage of the centrifugal current spilling over the panel edge. By increasing this centrifugal current by screening the edges of the panel from direct impingement, the 'edge effect' was accentuated.

ORIENTATION OF YOUNG AND OLD INDIVIDUALS

The influence of current on the orientation of barnacles approaching mature

size is well marked, but experiments on cyprids settling in water currents in the laboratory (Crisp 1955) failed to give other than a very weak orientation, which could only be demonstrated if the cyprids settled in darkness. This might have been due to unnatural conditions of settlement in the laboratory, so the orientation of very young spat and unmetamorphosed cyprids was compared with the orientation of adults under the same conditions in the field. Table 4 gives a number of results for *Balanus balanoides* and *Elminius modestus* belonging to different size-groups which settled under the same or closely similar conditions. It will be noted that in both species the young spat show little or no orientation to the current; their resultant orientation is vertically upwards or nearly so towards the light. There is no evidence of any appreciable change in orientation at metamorphosis.

The measurement of orientations of different age-groups settled under the same conditions shows generally an increasing orientation to the current with increasing size of the population. This is true both of *E. modestus* and *Balanus balanoides* and applies when the population is orientated to light, and, though less conclusively, when it has settled in conduits in darkness. The conclusion to be drawn from these results is that orientation to current at the time of settlement is negligible, but that during growth the barnacle rotates progressively so that it beats into the current. In this respect *B. balanoides* and *Elminius modestus* behave similarly to barnacles with basal canals, such as *Balanus improvisus*.

CHANGES IN ORIENTATION DURING METAMORPHOSIS

Experiments were carried out to ascertain when this change of orientation takes place. The behaviour of the metamorphosing cypris in water currents was first observed in the laboratory. In essentials the process appeared similar to that described more fully by Doochin (1951). Cyprids of *B. balanoides* were used on account of their large size which makes them easy to observe under a low-power binocular microscope.

The cypris stage of *B. balanoides* cements itself by the antennules after an exploratory phase, and remains quiescent for 24-30 hours as shown in Fig. 5, *A*. It is still covered by the bivalve carapace which is thick, leathery and slightly hydrofuge, and may therefore reduce water loss. During the quiescent phase a short muscular peduncle is developed which is apparently responsible for the renewed activity which Knight-Jones & Crisp (1953) described as marking the onset of metamorphosis (Fig. 5, *B*). The long axis of the cypris is slowly tilted so that its hind end becomes vertical (*C*). The bivalve carapace together with the apodemes of the paired eyes are shed in the course of slow rolling movements of the body on the peduncle (*D*). The body is now almost spherical (*E*). Having apparently rolled forwards on the peduncle, the median (naupliar) eye lies towards the posterior end of the body where it divides into two (Fales 1928, Doochin 1951). The rudiments of the parietal plates and valves appear and the animal is now recognizable as a small barnacle. The peduncle shortens and broadens and draws the sides of the barnacle down on to the substratum where they become cemented

(*F*). It will be noted that the peduncle and antennules are placed at the extreme anterior end of the barnacle at the time of fixation, but later the point of attachment lies roughly midway along the axis owing to the body rolling forward during metamorphosis. Hence water currents flowing over the cypris before metamorphosis will exert a torque tending to rotate the barnacle to face into the current,

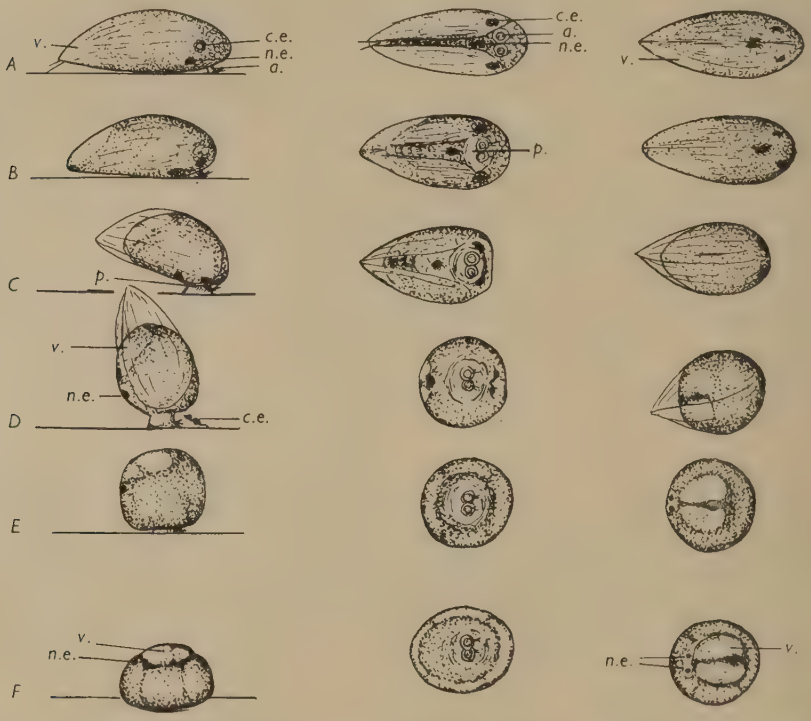

Fig. 5. Changes in external appearance of the larvae of *B. balanoides* during metamorphosis. Left, side view; middle, view from below through transparent substratum; right, view from above. *A*, immediately after attachment; *B*, end of quiescent phase (*ca* 24 h); *C*, beginning of metamorphic movements, tilting of body forwards (*ca* 25 h); *D*, further tilting followed by loss of carapace and apodemes (*ca* 25½ h); *E*, division of naupliar eye complete and peduncle shortened (*ca* 27 h); *F*, small barnacle pulled down on to substratum (*ca* 36 h). The eyes and valve rudiments are useful reference points in following changes of orientation.
a., antennular sucker; *c.e.*, compound eye; *n.e.*, naupliar eye; *p.*, peduncle; *v.*, valve rudiments.

though it seems usually able to resist this force (Crisp 1955). After metamorphosis this torque cannot be applied since the barnacle is pivoted about half way along its length. Finally the parietes and valves harden, the whole basal surface becomes firmly attached so that the peduncle disappears, and the cirri protrude through the space between the valves. It was noticed that the stage between the onset of metamorphic movements and the hardening of the cuticle after metamorphosis was very susceptible to desiccation. Many partially metamorphosed individuals

were observed to have dried out and collapsed if a plate were kept out of water for a few hours, while the metamorphosed individuals were unharmed.

The effect of water currents on metamorphosing cyprids was tested by playing a jet of water on them and observing their behaviour through a low-power binocular microscope. A thick glass plate covering the water surface is necessary to obtain good definition. The jet had a bore of approximately 1 mm and was directed at a low angle on to a flat plate on which the cyprids were attached, a few centimetres away from them; the rate of flow through the jet could be raised to a linear velocity of about 300 cm/sec, and it was estimated that the flow past the cyprids must have been in the order of 100-150 cm/sec. When cyprids had

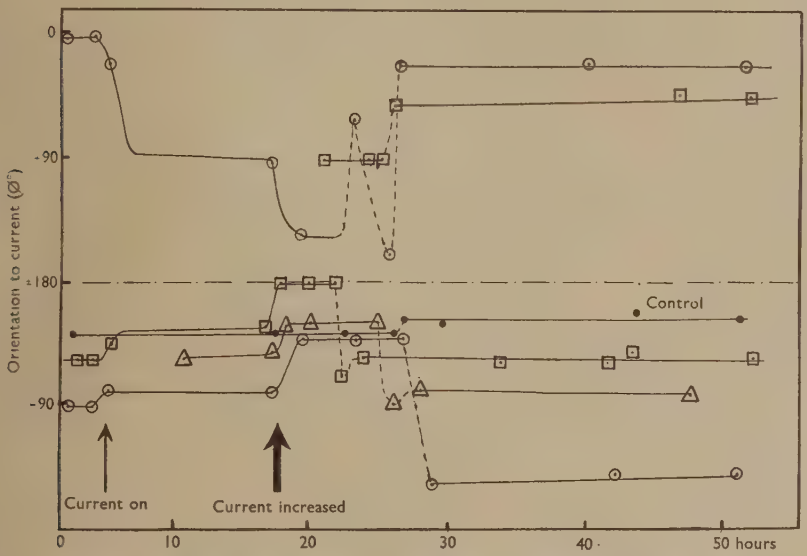

Fig. 6. Changes in orientation during metamorphosis under the influence of strong water currents. Each line represents the behaviour of one individual. The dotted section of the line represents movements during metamorphosis. The figure shows that the changes during the quiescent phase (0-24 h) all tended to align the cyprids passively to the current (increase in φ). Changes occurring during metamorphosis (*ca* 24-30 h) tended to restore the barnacle to its original position (decrease in φ). The control individual was not subjected to current.

just attached they tended to resist the torque caused by the jet when it was played on them from the side, but they could be swung by the maximum flow into a position with the anterior attached end upstream. On releasing the pressure by reducing the water current they slowly returned towards their original position. If they were deflected by the jet during the quiescent phase they did not return so well to their original position, but would frequently revert to it later during metamorphosis.

Once metamorphic movements began, the carapace protruding from the raised posterior end of the cypris was rather easily deflected by the current, dragging

the cypris round with it. However, as soon as the carapace was shed, the animal was able to take up a position more or less independent of the direction of the current, but not necessarily the position assumed by the cypris before metamorphosis. Indeed the orientation after metamorphosis not infrequently differed from that before by up to 30 or 40° (Fig. 6). This change did not show any consistent relationship to the direction of the current, though there was a slight tendency for the swing to bring the carinal end towards the downstream side of the current.

When metamorphosis was completed, the influence of the jet on orientation of the long axis of the barnacle was small. Instead the current tended to push the barnacle over on its side. If a strong jet were applied for a period the small barnacle was not only pushed over, but its peduncle severely stretched, giving it the appearance of a balloon tugging on a string (Fig. 7). The distortion rectified itself if the current was reduced in time. If the current were continued for several

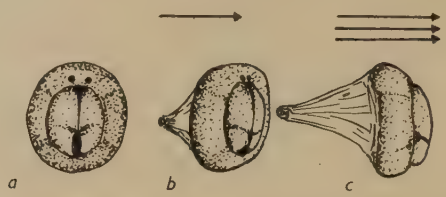

Fig. 7. Distorting effect of strong water currents on recently metamorphosed barnacles by extension of the peduncle. *a*, no current; *b*, moderate current; *c*, very strong current.

hours during which time the shortening of the peduncle and hardening of the cuticle would normally have taken place the barnacle seemed to be permanently distorted and eventually became detached.

CHANGES IN ORIENTATION AFTER METAMORPHOSIS

It was not possible to obtain satisfactory growth of barnacles in the laboratory water supply, which had previously been deprived of most of its suspended matter in settling tanks. Experiments were therefore made on a swivel device suspended from a raft in the Menai Straits. Eight rectangular bakelite panels measuring 10×15 cm were first exposed to settlement in the intertidal zone among an established population. When sufficient cyprids and young spat had settled on them the panels were photographed on fine grain plates and placed on the swivel in the sea, so that they were exposed to unidirectional flow. The plates were temporarily withdrawn from the sea after short intervals of time and re-photographed. From the photographs changes in orientation could be measured without any danger of disturbing the small barnacles. Satisfactory series of photographs were obtained from seven of the eight plates, and the average changes in orientation, $\Delta\Theta$, are given in Table 5. Positive values of $\Delta\Theta$ refer to changes which bring the posterior end of the barnacle towards the current source. The results show

considerable variation between the plates according to their position on the swivel, yet in all but one of the observations the change is in the expected sense. The exception is moreover not significant as it lies within twice the standard error. Furthermore, variations in the average change of orientation among the plates, which can be seen to be significant from the analysis of variance, affect the degree of rotation similarly throughout the whole period of growth. Thus plates 1 and 7 which show the least rotation during period A show small rotations in growth-periods B and C even though different groups of individuals were measured. Similarly panels 4, 6 and 8 showed exceptionally large rotations throughout.

Table 5. *Changes in orientation during growth of* B. balanoides

Plate Number	Changes in orientation, $\Delta\Theta$, in degrees with standard errors during A growth from cypris to barnacle 2·0 mm diam.	B growth from recently metamorphosed barnacle 1·2 mm diam. to barnacle 2·2 mm diam.	C growth from barnacle 2 mm diam. to barnacle 3·5 mm diam.
1	6·7 ±5·8	9·3 ±3·4	−2·4 ±1·5
2	13·9 ±8·3	9·0 ±2·9	8·6 ±2·3
3	15·9 ±4·5	5·9 ±2·9	4·25 ±2·1
4	33·4 ±18·6	19·5 ±2·4	15·6 ±2·7
6	35·0 ±8·3	20·1 ±4·2	11·5 ±4·9
7	4·5 ±4·1	2·9 ±3·5	4·6 ±3·5
8	37·0 ±11·6	21·2 ±4·2	13·9 ±4·3
Mean	20·9 ±3·3	12·6 ±1·8	8·0 ±1·5

Analysis of variance of orientation changes under columns A, B and C above:

		Sum of squares	Degrees of freedom	Mean square
Between plates	A	11 589	6	1931·5
	B	3 407	6	567·7
	C	2 382	6	396·9
Between individuals on plates	A	42 393	63	672·9
	B	12 176	63	193·3
	C	8 862	63	140·7

Many of the individual values and all the mean values of rotation are significantly positive, showing the tendency to rotate the cirri into the current. In Table 6 these average changes of orientation are shown against the size of the barnacle. The average change in orientation at metamorphosis is clearly small, perhaps negligible. As growth begins, however, rotation takes place, rapidly at first in the young barnacle, and then more slowly.

CONCLUSIONS

In a previous publication Crisp (1953) concluded that only those barnacles which had basal canals showed appreciable rotation during growth. This was because in *Balanus balanoides*, *Elminius modestus* and *Balanus crenatus* no changes

in orientation had been found to occur under natural conditions (Barnes, Crisp & Powell 1951) whereas in *B. improvisus* and *B. amphitrite* twisting of the radial canals, indicating rotation, was usual. It is now clear that no such difference can be entertained, though it is possible that species with radial canals may rotate more readily. All species which have now been exposed to unidirectional current, whether they have canals in the basis or not, show rotation during growth, the cirral net being brought round to face into the current.

There appears to be no clear response by the cypris to water currents either at the time of fixation nor during the ensuing movements effecting metamorphosis. The influence of current therefore differs from the influences of light and surface contour, for these latter evoke definite reactions at the time of fixation (Barnes, Crisp & Powell 1951, Knight-Jones & Crisp 1953, Crisp & Barnes 1954). The slight effect of water current noted by Crisp (1955) in a large population of cyprids which had recently metamorphosed represented most probably a small degree of rotation,

Table 6. *Mean changes in orientation in relation to size of barnacle*

Average size	Average change in orientation, $\Delta\Theta$	Total rotation	Average rate of rotation with growth along rostro-carinal diameter
Cypris (0·9 mm)	–	0	
1·2 mm	+8·3°	8·3°	27·6° per mm
2·2 mm	+12·6°	20·9°	12·6° per mm
3·5 mm	+8·0°	28·9°	6·1° per mm

for rotation takes place most rapidly immediately after metamorphosis when the young barnacle is most malleable.

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SUMMARY

1. Adult populations of *Balanus balanoides*, *B. crenatus* and *Elminius modestus* are orientated by a water current so that the majority have the carinae pointing away from the current source and the cirral net facing the current.

2. Naturally occurring populations of *Coronula diadema* take up the same orientation in respect of the flow of water past the whale host on which they are found.

3. The cypris usually orientates at first towards the light. This orientation is then modified by the water currents during growth. Since the light generally falls vertically and the current flows horizontally, the barnacles slowly rotate from a predominantly vertical position when young to a tilted or nearly horizontal position when adult. The orientation of barnacles on the hulls of moored craft can usually be explained by the dual influence of light and current.

4. There is no appreciable influence of water currents on the cypris at the time of fixation or during metamorphosis.

5. Current influences orientation throughout the growth of the metamorphosed barnacle, and its effect is greatest in the very early stages of growth.

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THE ECOLOGY OF THE LOUGH INE RAPIDS WITH SPECIAL REFERENCE TO WATER CURRENTS

V. THE SEDENTARY FAUNA OF THE LAMINARIAN ALGAE IN THE LOUGH INE AREA

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(With 12 Figures in the Text)

Lough Ine, in County Cork, Ireland, is a sea lough which is connected to the Atlantic by Barloge Creek, about $\frac{3}{4}$ mile long. At the junction of the Creek and the Lough is the shallow and narrow Rapids. Accounts of the tidal phenomena and of the resultant changes in chemical and physical conditions in the Rapids have

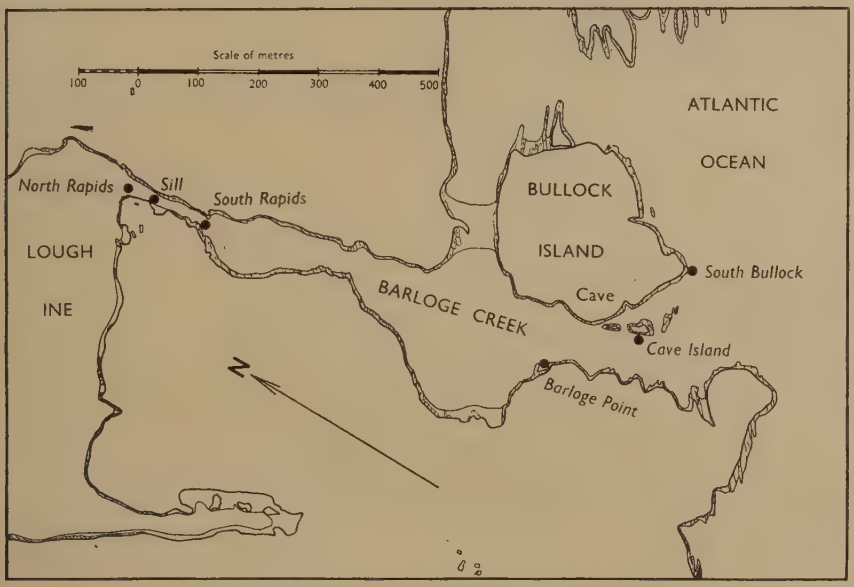

Fig. 1. Map of the Rapids and Barloge Creek to show stations.

been given in previous papers of this series (Bassindale *et al.* 1948, Kitching *et al.* 1952). The rocky floor of the Rapids is covered with Laminarian algae of which *Saccorhiza polyschides* Batt. (Parke 1953)* is the most plentiful. An account of

**Saccorhiza bulbosa* De la Pyl. (Newton 1931).

the associated sedentary fauna throughout the Rapids and of current at the level of the canopy of fronds has already been given (Ebling *et al.* 1948). The present paper describes an investigation of the fauna associated with *S. polyschides* and other laminarian algae in Barloge Creek and on the open coast. The object of

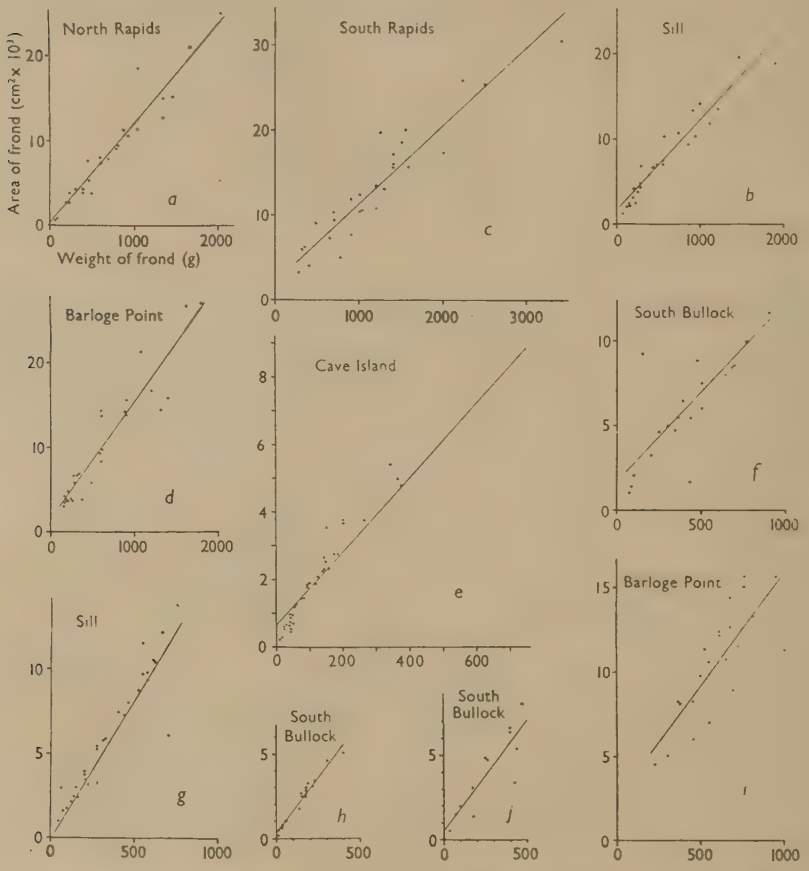

Fig. 2. Scatter diagrams of frond area plotted against weight with calculated rectilinear regressions. *a-f, Saccorhiza polyschides; g, h, Laminaria digitata; i, j, L. hyperborea.*

the survey was to compare regions exposed to different amounts of wave-action with stations subjected to known water currents in the Rapids. The work was carried out by members of an expedition in July 1951.

STATIONS

Algae were collected by a diver in a frog suit from depths ranging from 1 to 5 m below low water ordinary spring tide. Fig. 1 is a map of the stations, three of

which were in the Rapids, two in Barloge Creek and one in the adjacent open sea. Details follow.

North Rapids. This station was situated a little to the north of point 1 (Bassindale *et al.* 1948, Fig. 1), about 4 m out from the quay, and had a depth of about 1·5 m below low slack water. At the level of the frond canopy the current reaches a maximum of about 1·5 m/sec during the inflow of spring tides (Ebling *et al.* 1948).

The Sill. This station extended a little southward from a point about 1-1·5 m out from the quay at point 4 (Bassindale *et al.* 1948, Fig. 1). The depth was about 1 m. Current speeds of up to 2 m/sec occur during outflow.

South Rapids. This station was situated towards mid-stream, well south of the main current. There was gentle turbulence at the bottom, causing the fronds to wave irregularly to and fro.

Table 1. *Frond weights and areas of* Saccorhiza polyschides, Laminaria digitata *and* L. hyperborea

Station	Number of plants	Frond weight (g)		Frond area (sq. cm)		Regression coefficient	Standard error	Fig. no.
		Range	Mean	Range	Mean			
Saccorhiza polyschides								
North Rapids	25	60–2 040	735	745–25 000	8 910	11·74	0·68	2*a*
Sill	26	78–1 870	584	1 285–19 600	7 842	10·67	0·83	2*b*
South Rapids	28	280–3 400	1 193	3 260–30 450	13 359	9·07	0·65	2*c*
Barloge Point	28	150–1 800	632	3 070–27 000	10 331	13·76	0·96	2*d*
Cave Island	37	10– 740	134	224– 7 280	2 095	11·15	0·62	2*e*
South Bullock	21	70– 900	423	1 060–11 700	6 235	10·76	1·94	2*f*
Laminaria digitata								
Sill	28	50– 740	357	1 008–13 800	6 275	15·57	1·15	2*g*
South Bullock	18	15– 400	168	151– 5 440	2 534	13·24	0·55	2*h*
Laminaria hyperborea								
Barloge Point	21	220–1 000	585	4 500–15 660	10 327	13·08	2·49	2*i*
South Bullock	12	35– 480	269	547– 8 100	3 996	13·15	2·41	2*j*

Barloge Point. This station, near the mouth of Barloge Creek, appeared to be rather sheltered from the waves, but not stagnant. The weeds were taken from two regions within one bay, and designated North group and South group.

Cave Island. The station was open to the Atlantic through a narrow angle formed by the mouth of Barloge Creek. It is probably subjected to a flow of water due to tidal movement in and out of the Creek and Lough.

South Bullock. The station was open to the Atlantic through a wide angle. It is subjected to considerable wave action, but the flow of water is presumably small.

THE LAMINARIAN ALGAE

Immediately after collection the algae were measured and then weighed on a spring balance. The frond areas were measured by the use of transparent grids ruled in centimetre squares.

The relationship of frond area to frond weight is shown in Fig. 2 and the results are summarized in Table 1. It is clear that the rectilinear regression coefficients

are sufficiently similar for all stations, for each of the three species studied (*Saccorhiza polyschides*, *Laminaria digitata* Lamour and *L. hyperborea* Fosl.*), for frond weight to be used as a proportional measure of frond area. It may, however, be

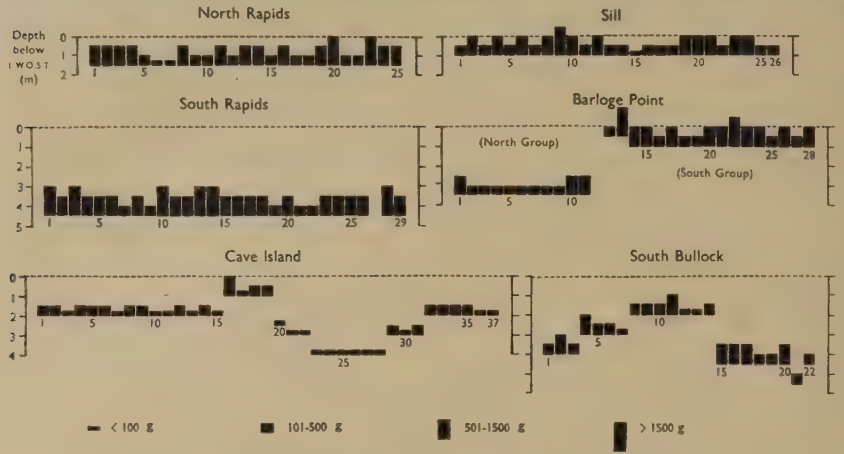

Fig. 3. Depth and frond weights of *Saccorhiza polyschides* at six stations. The lower edge of each block indicates the depth at which the alga was collected.

noted that there appear to be small but significant differences between some of the coefficients. For example, fronds of *Saccorhiza* from Barloge Point appear to weigh less per unit area than fronds from South Rapids or the Sill; this may reflect a difference in the growth of the plants. In Fig. 3 both the depths and individual frond weights (in categories) are shown diagrammatically.

THE EPIPHYTIC ALGAE

Records were made by Dr S. M. Lodge of the epiphytic algae on the frond and

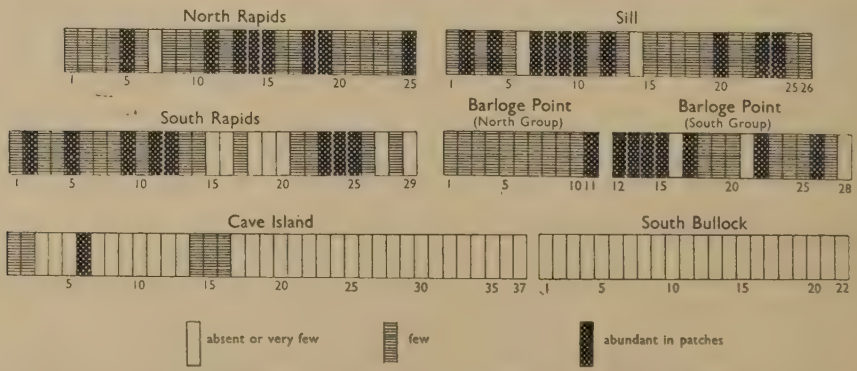

Fig. 4. The distribution of epiphytes on the fronds of *Saccorhiza polyschides*.

stipe of each *Saccorhiza* plant, and the total abundance of epiphytes on the fronds was also estimated by her in terms of a subjective scale as follows: (1) 'none' or

**Laminaria cloustoni* Edmonst. (Newton 1931).

'very few', (2) 'few', (3) 'abundant in patches', (4) 'abundant all over'. The results are shown in Fig. 4.

Ectocarpus was the commonest epiphyte on the fronds and stipes of *Saccorhiza*. At least two species were found. *Ectocarpus* was noted on only two of the fronds from South Bullock, but was found on many of the fronds at each of the other stations. The other epiphytes noted are *Litosiphon* sp., *Callithamnion brachiatum*, *Ceramium* sp., and *Enteromorpha* sp. *Litosiphon* was found on many fronds at each of the three stations in the Rapids. No epiphytes other than *Ectocarpus* were reported from fronds or stipes at South Bullock.

THE FAUNA

The fauna of the algae was studied either in the field or in the laboratory immediately after collection. The abundance of each species was recorded in one of three ways. For some species (e.g. *Patina pellucida*) it was possible to count the number of individuals; for others (e.g. *Hippothoa hyalina* and *Tubulipora* sp.) the number of colonies was counted. Other species (e.g. *Membranipora membranacea*), which did not lend themselves to either of these methods, were treated by assessing the percentage area of the frond covered.

(*a*) *The fauna of* Saccorhiza polyschides

Seven species of sedentary animals occurred frequently on *Saccorhiza polyschides*, namely the hydroids *Obelia geniculata* L. and *Tubularia bellis* Allman, the Polyzoa *Hippothoa hyalina* (L.), *Membranipora membranacea* (L.) and *Tubulipora* sp., the tube-building amphipod *Jassa falcata* (Montagu), and the gastropod *Patina pellucida* (L.). The distribution of these animals is shown in Figs. 5-11. The topographical preferences of these common species can be summarized as follows:

Obelia geniculata (Fig. 5) occurred sparsely at all stations and was recorded from all parts of the alga (fronds, stipes, frills at base of stipes, and holdfasts) with a preference for fronds.

Tubularia bellis (Fig. 6) occurred only in the Rapids area. It was abundant at North Rapids and Sill, sparse at South Rapids, and was absent, except for a single occurrence at Barloge Point, from the three seaward stations. It was found mainly on frills and holdfasts and only rarely on the flat region of the stipe or on the fronds.

Hippothoa hyalina (Fig. 7) occurred abundantly at all stations except South Bullock. It was found with equal abundance on all parts of the algae at South Rapids and Barloge Point (South group), but at North Rapids, Sill, and Cave Island it was mainly restricted to the frills and holdfasts and occurred only rarely and sparsely on the fronds. At South Bullock and at Barloge Point (North Group) it was recorded sparsely from frills and holdfasts only.

Membranipora membranacea (Fig. 8) occurred much more abundantly at the three stations in the Rapids than at the seaward stations. Although it was extremely abundant on fronds, flats, and frills at North Rapids and South Rapids

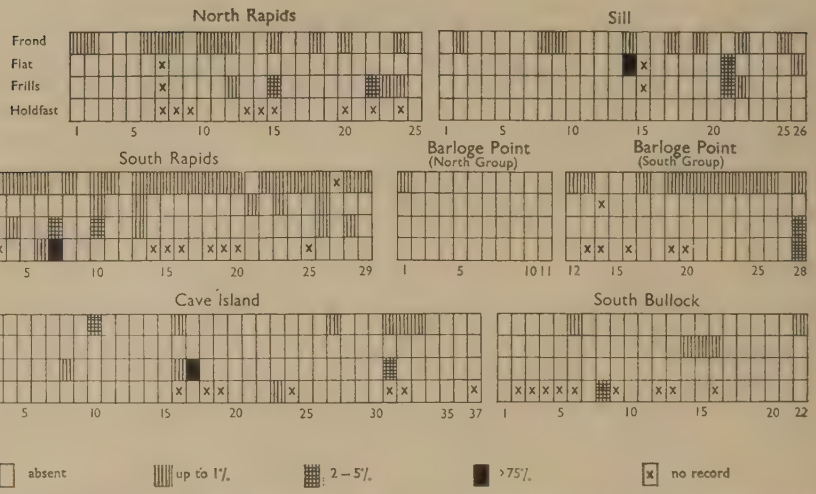

Fig. 5. The distribution of *Obelia geniculata* on the fronds, on the flats and frills of the stipes, and on the holdfasts of *Saccorhiza polyschides*. Quantities are expressed as percentage area covered.

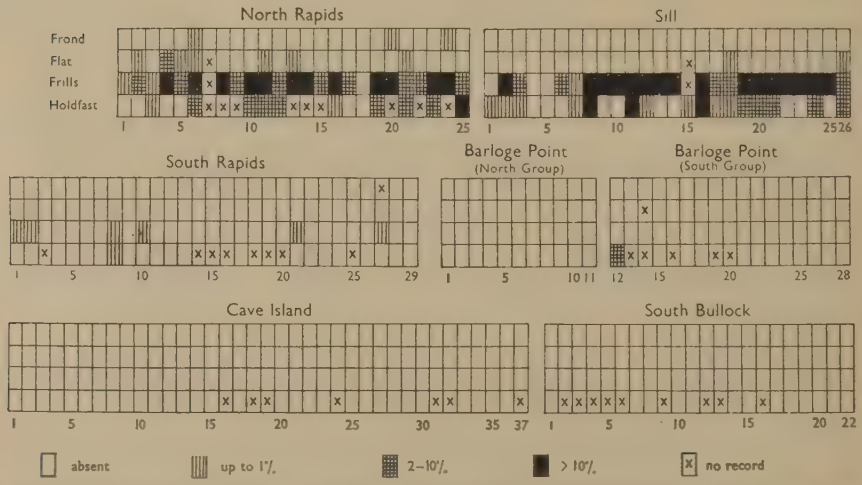

Fig. 6. The distribution of *Tubularia bellis* on *Saccorhiza polyschides*; quantities as percentage area covered.

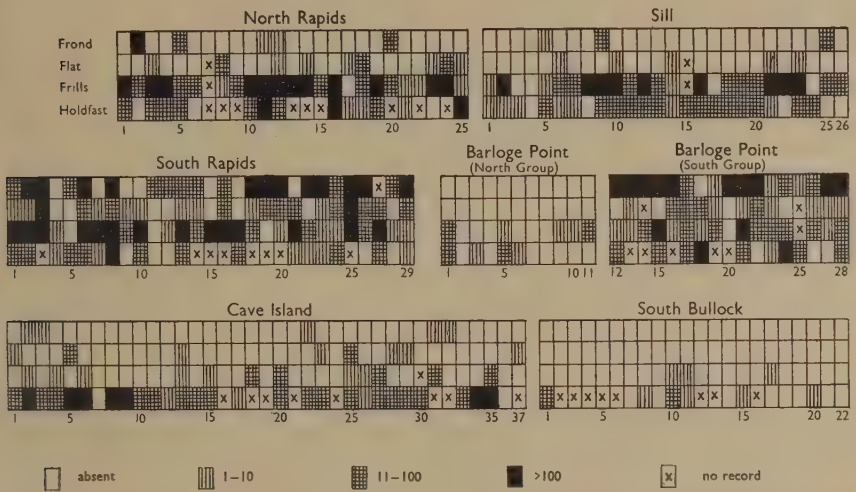

Fig. 7. The distribution of *Hippothoa hyalina* on *Saccorhiza polyschides*. Quantities are numbers of colonies.

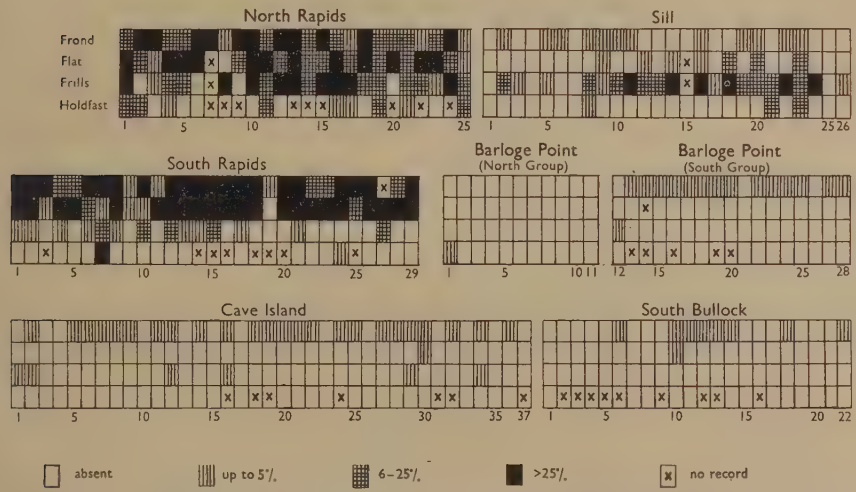

Fig. 8. The distribution of *Membranipora membranacea* on *Saccorhiza polyschides*; quantities as percentage area covered.

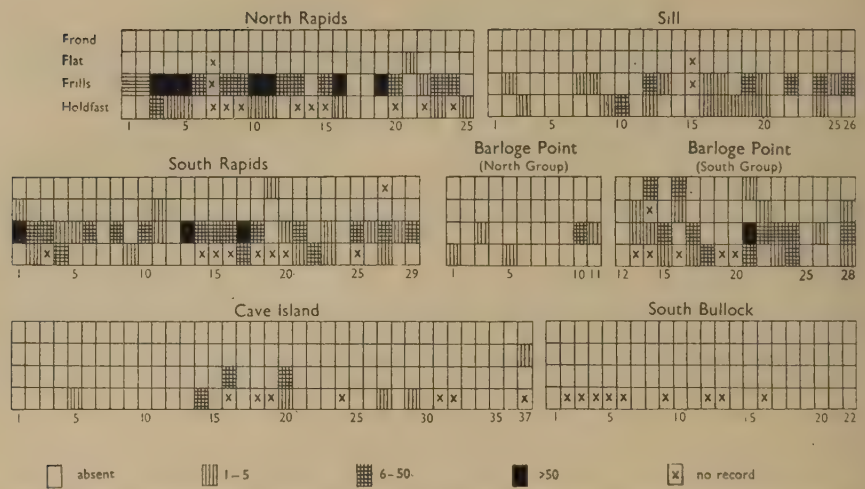

Fig. 9. The distribution of *Tubulipora* sp. on *Saccorhiza polyschides*. Quantities are numbers of colonies.

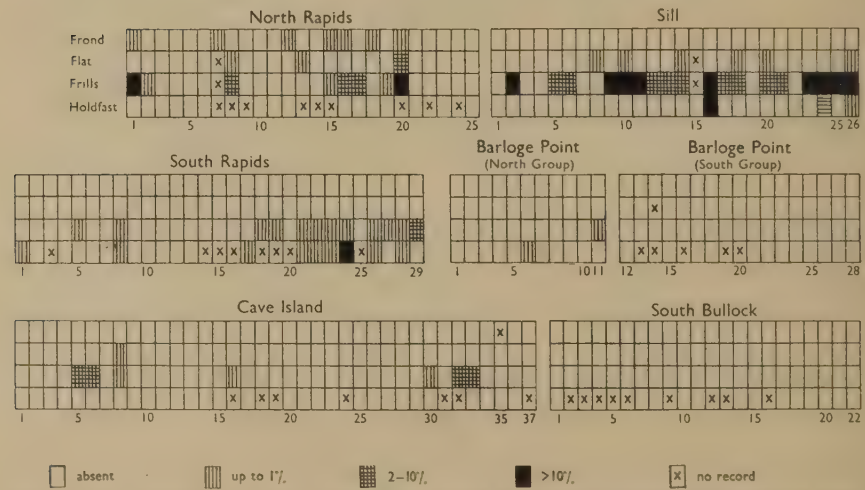

Fig. 10. The distribution of *Jassa falcata* on *Saccorhiza polyschides*; quantities as percentage areas covered by the tubes.

at the Sill it was mainly confined to the frills, and was only sparsely recorded from the flats and fronds. At the seaward stations it occurred sparsely but frequently on the fronds and only rarely on other parts of the algae.

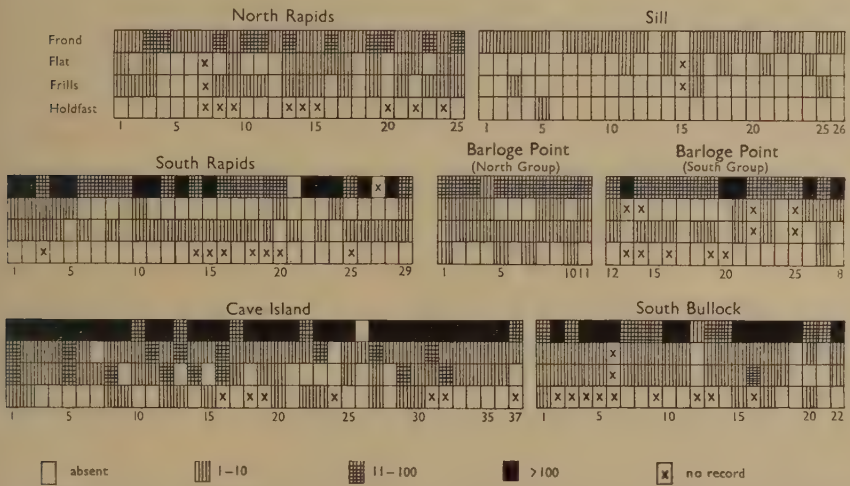

Fig. 11. The distribution of *Patina pellucida* on the fronds, flats and frills of the stipe, and the holdfasts of *Saccorhiza polyschides*. Quantities are numbers of individuals.

Tubulipora sp. (Fig. 9) occurred abundantly at North Rapids and South Rapids, a little less plentifully at Barloge Point (South group), in moderate amounts on the Sill, and more rarely at Barloge Point (North group) and at Cave

Table 2. *Occurrence of rarer species on fronds of* Saccorhiza polyschides

The figures show the number of plants at each station on which the animals occurred; in parentheses is shown the greatest number of individuals or the maximum percentage area covered on any one plant.

	North Rapids	Sill	South Rapids	Barloge Point	Cave Island	South Bullock
Number of plants examined	25	26	28	28	37	22
Sertularia operculata L.	0	0	1 (<1%)	0	0	0
Anemone	0	0	1 (1)	0	0	0
Costazia costazii (Aud.)	0	0	0	1	0	0
Scruparia chelata (L.)	0	0	12 (<1%)	0	5 (<1%)	0
Scrupocellaria reptans (L.)	0	0	1 (<1%)	0	0	0
Caprellidae	0	2	0	0	0	0
Polycera quadrilineata (O. F. M.)	1 (1)	0	7 (150)	0	0	0
Rissoa parva (da Costa)	0	0	0	1 (4)	0	0
Mytilus edulis L.	0	3 (1)	0	0	0	0
Tunicates*	0	0	1 (<1%)	2 (<1%)	0	0

* One specimen from Barloge Point identified as *Botryllus schlosseri* (Pallas).

Island. It was absent from South Bullock. It occurred mainly on frills and holdfasts.

Jassa falcata (Fig. 10) occurred abundantly on the Sill and in moderate amounts

at North Rapids and South Rapids. It was rare at Barloge Point (North group) and at Cave Island, and absent from Barloge Point (South group) and South Bullock. It was found mainly on frills and holdfasts.

Patina pellucida (Fig. 11) was much more abundant at South Rapids and at the three seaward stations than at the Sill or North Rapids. It was found on all parts of the algae, but the greatest numbers were recorded from the fronds.

The distribution of ten species which occur rarely is summarized, for fronds only, in Table 2. The information is insufficient to lead to any useful conclusion about individual species, but it is worth noting that the largest number of species occurred at South Rapids and Barloge Point. Two kinds of animals (*Mytilus edulis* and Caprellids) occurred on the Sill and at no other station; none of the ten species occurred at South Bullock.

(*b*) *The fauna of the fronds of* Laminaria digitata *and* L. hyperborea

The distributions of six species on the fronds of *L. digitata* at Sill and South Bullock and of eight species found on fronds of *L. hyperborea* at Barloge Point and South Bullock are summarized in Table 3. There is no reason to conclude from the evidence that the fronds of *L. digitata* or *L. hyperborea* compare favourably or unfavourably with *Saccorhiza* as substrates for any of the species

Table 3. *Fauna of the fronds of* Laminaria digitata *and* L. hyperborea

The figures show the number of plants at each station on which the animals occurred; in parentheses is shown the greatest number of individuals or colonies or the maximum percentage area covered on any one plant.

Laminaria digitata	Sill	South Bullock
Number of plants examined	28	34
Obelia geniculata	1 (<1%)	3 (<1%)
Hippothoa hyalina	2 (45)	0
Membranipora membranacea	0	11 (<1%)
Jassa falcata	1 (<1%)	0
Mytilus edulis	3 (3)	2 (1)
Patina pellucida	2 (1)	30 (33)

Laminaria hyperborea	Barloge Point	South Bullock
Number of plants examined	21	12
Obelia geniculata	13 (1%)	10 (2%)
Sertularia operculata	1 (<1%)	0
Hippothoa hyalina	4 (<1%)	0
Eucratea chelata (L.)	1 (1)	0
Membranipora membranacea	12 (5%)	3 (1%)
Hiatella arctica (L.)	1 (1)	0
Anomiids	1 (1)	0
Patina pellucida	21 (80)	12 (53)

listed except *Patina pellucida*. It is true that on the Sill *Obelia geniculata* was found on only 1 out of 28 plants of *Laminaria digitata*, but on 8 out of 26 of *Saccorhiza polyschides*, and that *Membranipora membranacea* did not occur on *Laminaria digitata* on the Sill but was recorded on about half the plants of *Saccorhiza*. No such differences could be detected at Barloge Point or South Bullock, and the results possibly reflect the greater exposure of *L. digitata* on the Sill.

(*c*) *The distribution of* Patina pellucida

The number of Patina was plotted against frond weight for each plant at each station and the scatter diagrams are shown in Fig. 12.

At any one station the number of *Patina* is very nearly proportional to frond weight, but tends to fall short for the heavier fronds. Dr G. H. Jowett and Miss Hilda Davies of the Department of Statistics of the University of Sheffield very kindly investigated the data to ascertain the best means of analysis. Parabolic regressions gave a slightly better fit than rectilinear ones passing through zero for the samples of *Saccorhiza polyschides* from North Rapids and Cave Island but not for the others, and reciprocal or logarithmic transformations did not help, so for convenience we have used ordinary rectilinear regressions throughout.

Table 4. *Distribution of* Patina pellucida *on* Saccorhiza polyschides, Laminaria digitata *and* L. hyperborea *in July 1951*

	Number of plants	Frond weight (g.)		Number of *Patina* per plant		Regression coefficient	Standard error	Fig. no.
		Range	Mean	Range	Mean			
Saccorhiza polyschides								
North Rapids	25	60–2040	735	1– 39	14·5	0·0106	0·0034	12*a*
Sill	26	78–1870	584	0– 10	2·7	0·0024	0·0026	12*b*
South Rapids	28	280–3400	1193	0–264	118·7	0·0667	0·0170	12*c*
Barloge Point	28	150–1800	632	8–180	60·6	0·0767	0·0136	12*d*
Cave Island	37	10– 740	134	0–829	264·3	1·0229	0·1541	12*e*
South Bullock	21	70– 900	423	6–621	212·1	0·3145	0·1430	12*f*
Laminaria digitata								
Sill	28	50– 740	357	0– 2	0·2	–	–	–
South Bullock	21	15– 400	161	0– 33	10·3	0·0141	0·0205	12*g*
L. hyperborea								
Barloge Point	21	220–1000	585	8– 82	37·7	0·0646	0·0185	12*h*
South Bullock	12	35– 480	269	4– 75	30·4	0·0202	0·0419	12*i*

The results are shown in Table 4. The regression coefficient for *Patina* on *Saccorhiza* at the Sill is not significantly different from zero, but there are obviously fewer *Patina* there than at any other station. The next lowest coefficient is that for North Rapids. The coefficient for South Rapids is clearly significantly greater, but that for Barloge Point is not significantly different from that for South Rapids. An examination of the mean numbers of *Patina* per plant and the mean frond weights confirms that the population density of *Patina* does not differ at these two stations. The density of *Patina* is obviously much higher at South Bullock and significantly greater again at Cave Island.

It is possible to compare the relative popularity of *Saccorhiza polyschides*, *Laminaria digitata* and *L. hyperborea* as substrata for *Patina* at South Bullock. Clearly the regression coefficient for *Patina* on *Laminaria hyperborea* is significantly lower than for *Patina* on *Saccorhiza*. It is also possible to compare the mean number of *Patina*, after correction for regression, by an analysis of covariance; this gives $F = 9{\cdot}0$ for 1,30 degrees of freedom ($P < 0{\cdot}01$). A similar analysis for *Patina* on *Laminaria hyperborea* and *L. digitata* gives $F = 13{\cdot}8$ for 1,30

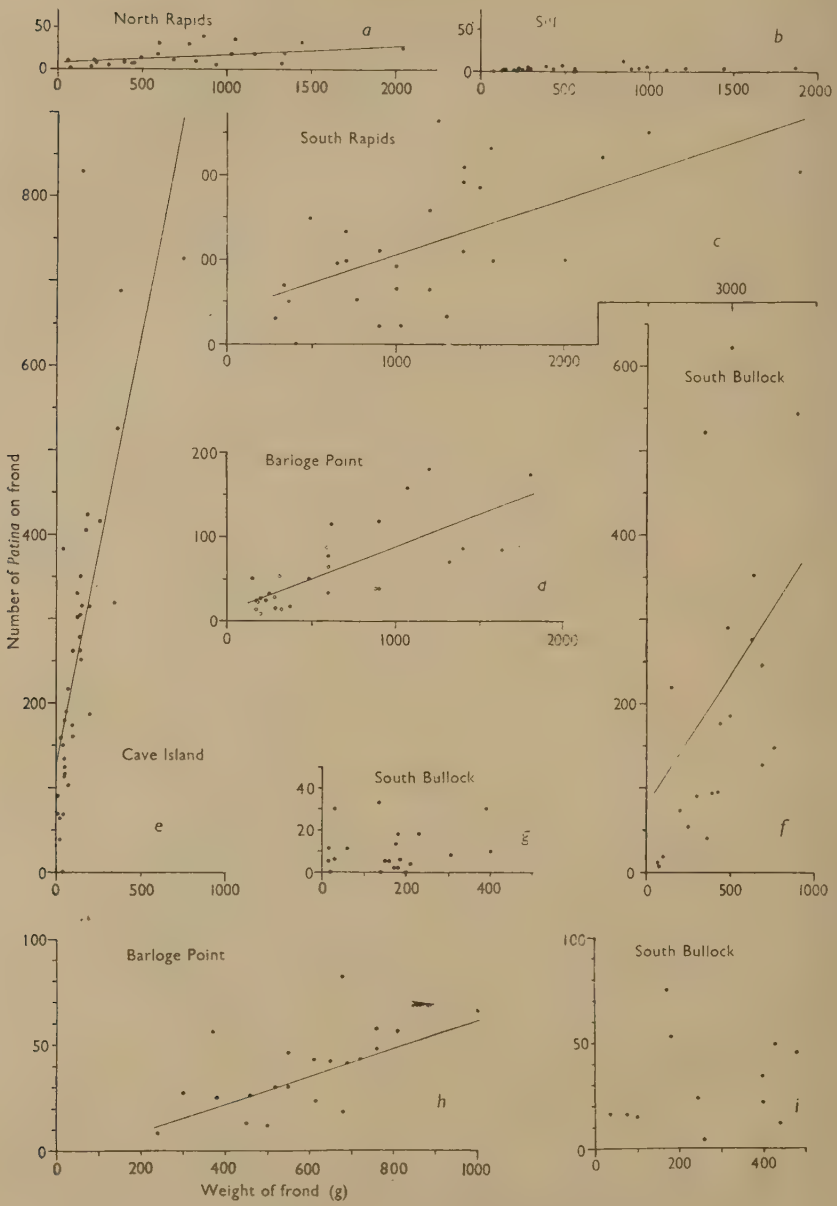

Fig. 12. Number of *Patina* and frond weight of—*a-f, Saccorhiza polyschides; g, Laminaria digitata; h, i, L. hyperborea.*

degrees of freedom ($P<0{\cdot}01$). It seems reasonable to conclude that the fronds of *Saccorhiza* proved a more favourable substratum for *Patina* than either of the other two algae, and this conclusion is supported by the data for the other stations studied.

DISCUSSION

The distribution of sedentary animals on *Saccorhiza polyschides* in relation to water currents in the Rapids area was previously studied in 1946 and 1947 (Ebling *et al.* 1948). It was then found that *Hippothoa hyalina* and *Tubulipora plumosa* favoured weaker currents; at the Sill and at other places exposed to current these species were present mainly in the frills of the stipes. *Membranipora membranacea* favoured moderate current, and *Jassa falcata* and *Tubularia bellis* favoured strong current but were confined to regions of the plant not directly exposed to it. The results of the 1951 survey are all entirely in keeping with these earlier records.

Our chief problem is to assess how far the effects of wave-action on the distribution of animals at the seaward stations resemble the effects of current in the

Table 5. *Current and wave-action at six stations shown in Fig. 1*

Station	Current	Wave-action
North Rapids	Fairly strong	None
Sill	Very strong	None
South Rapids	Moderate	Almost none
Barloge Point	Very slight	Slight
Cave Island	Slight but probably continuous	Moderate
South Bullock	Slight	Strong

Rapids area. The answer is bound to be tentative because currents at the seaward stations have not been measured, and we have no quantitative information about wave-action. However, an attempt has been made to summarize the main features of current and wave-action at the stations in Table 5. Our experience of this area is so far limited to the summer months, and we recognize that events at other seasons may profoundly affect the situation.

For two species, *Hippothoa hyalina* and *Tubulipora* sp., the distribution at the seaward stations appears to be related to wave-action just as the distribution in the Rapids area is related to current. It is interesting that of the seven common species under consideration, these are the only two which prefer weaker currents. In the Rapids area both these species are much less abundant on the Sill than at North or South Rapids, and on the Sill both are mainly confined to the frills and holdfasts. At the seaward stations both show a progressive and drastic decrease towards the open coast, and both show a similar restriction towards the frills and holdfasts as they die out. Some of the possible effects of current have already been discussed in a previous paper (Lilly *et al.* 1953). It seems likely that in this case water movements either prevent the settling of larvae or dislodge the settled organisms.

Three species, namely *Tubularia bellis*, *Membranipora membranacea*, and *Jassa falcata*, had a marked preference for the Rapids area but were absent from, or sparse at, all the seaward stations. As these are all species which have been shown to favour moderate or strong currents within the Rapids area, it seems either that the favourable effects of current are not produced by wave-action or that there is another overriding factor which causes these species to prefer the Rapids area. For instance, it is possible that the continuous current of the Rapids area provides unusually favourable feeding conditions or that physical or chemical conditions resulting from the outflow of Lough water are more advantageous. Various suggestions of this kind could be made, but further investigation will be needed both in the field and in the laboratory before this matter can be settled.

Finally one species, *Patina pellucida*, had a marked preference for South Rapids and the three seaward stations to North Rapids and the Sill. The results of the present survey confirm our previous conclusion (Ebling *et al.* 1948) that in the Rapids area *Patina* prefers a moderate current. They add, however, the important fact that the numbers of *Patina* were much greater at South Rapids and at all the seaward stations than at North Rapids or Sill. The greatest numbers were at Cave Island, so that moderate wave-action appears to favour *Patina* in the sea just as moderate current does in the upper Rapids, but it also appears that some additional adverse factor supervenes from the Sill northwards. Again, various suggestions might be made. For instance, the current flows almost continuously on the Sill and at North Rapids, whereas at South Rapids there are much longer periods of relatively quiet water with slow turbulent movement rather than continuous flow. It is possible that the opportunities for the settlement of *Patina* are much more restricted at North Rapids and the Sill than anywhere else.

There is no evidence that differences in depth had any significant influence on the fauna within the narrow range of depths over which we worked.

ACKNOWLEDGMENTS

This work was carried out by means of an expedition from the Department of Zoology, University of Bristol, and we are glad to acknowledge the full support of Professor J. E. Harris, F.R.S. We are grateful to Professor L. P. W. Renouf and to University College, Cork, for the use of the Marine Biological Station, Lough Ine. Valuable financial help was received from the Colston Research Society and the University of Sheffield Research Fund. The diving equipment was bought by a grant from the Royal Society. We wish to thank Dr G. H. Jowett and Miss Hilda Davies of the Department of Statistics, University of Sheffield, for help and advice in statistics. We are also indebted to Mr G. Wing and members of the technical staff of the Department of Zoology, University of Bristol.

The following took part as students in the field work: Elisabeth Davenport, Audrey R. Fisher, J. G. Hay, Anne M. Legg, A. J. Lucas, J. H. Peters, Patricia M. Scholes, M. A. Sleigh, P. Tuley, Eileen G. C. Walden, Catherine A. Young. Professor E. Percival of Canterbury College, New Zealand, and Dr Sheila M.

Lodge of the Marine Biological Station, Port Erin, were also members of the expedition. Catering was carried out by Erika Ebling.

We should also like to acknowledge the help of Professor R. D. Purchon both in the field work and in the identification of Mollusca in a previous investigation (Lilly *et al.* 1953).

SUMMARY

1. Plants of *Saccorhiza polyschides*, *Laminaria digitata* and *L. hyperborea* were collected from three stations in the Lough Ine Rapids and three stations subjected to different amounts of wave-action in the adjacent Barloge Creek and on the open coast.

2. From measurements of algal frond weight and frond area it was concluded that, although minor differences exist between some stations, frond weight is a satisfactory proportional measure of frond area.

3. Two species of animals, *Hippothoa hyalina* and *Tubulipora* sp., favoured weaker currents in the Rapids and were found also in regions comparatively sheltered from wave-action. It is suggested that both current and wave-action affect these species unfavourably.

4. Three species, *Tubularia bellis*, *Membranipora membranacea* and *Jassa falcata*, favoured moderate or strong currents within the Rapids, but were absent from or sparse at all the seaward stations. It is suggested that current has some favourable effect, such as the provision of planktonic food, which is not possessed to the same extent by wave-action, although other explanations are possible.

5. *Patina pellucida* favoured moderate current in the Rapids and moderate wave-action in the sea, but was much more plentiful at all the seaward stations. Perhaps current restricts settlement in the Rapids.

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Bassindale, R., Ebling, F. J., Kitching, J. A. & Purchon, R. D. (**1948**). The ecology of the Lough Ine Rapids with special reference to water currents. I. Introduction and hydrography. *J. Ecol.* **36,** 305-22.

Ebling, F. J., Kitching, J. A., Purchon, R. D. & Bassindale, R. (**1948**). The ecology of the Lough Ine Rapids with special reference to water currents. II. The fauna of the *Saccorhiza* canopy. *J. Anim. Ecol.* **17,** 223-44.

Kitching, J. A., Lilly, S. J., Lodge, S. M., Sloane, J. F., Bassindale, R. & Ebling, F. J. (**1952**). The ecology of the Lough Ine Rapids with special reference to water currents. III. The effect of current on other environmental conditions. *J. Ecol.* **40,** 179-201.

Lilly, Sylvia J., Sloane, J. F., Bassindale, R., Ebling, F. J. & Kitching, J. A. (**1953**). The ecology of the Lough Ine Rapids with special reference to water currents. IV. The sedentary fauna of sublittoral boulders. *J. Anim. Ecol.* **22,** 87-122.

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REVIEWS

THE YEAR'S ENTOMOLOGY

E. A. Steinhaus (Editor). *Annual Review of Entomology*, Vol. 1, 1956. Pp. x+466; 7 plates; 2 text-figs. Stanford, Calif.: Annual Reviews Inc. Price $7.50.

The ever increasing spate of scientific papers on insects makes summaries of rapidly advancing fields desirable from time to time, and the appearance of a new periodical planned to satisfy this need is therefore very welcome.

Volume 1 contains twenty-one review articles on a wide variety of topics, nine of which are concerned with the use of insecticides or repellants in crop protection. Of these, ecologists will find Dr Ripper's informative review of the effects of pesticides on the balance of arthropod populations of special interest. The many cases now known in which pests have increased after spray treatments, or have developed strains resistant to the insecticide are documented by the citation of over 200 references. The author examines ways in which the unfavourable long term effects can be avoided by devising sprays or methods of application which preserve predators or parasites to the greatest extent.

Dr S. A. Graham of Ann Arbor writes on the ecology of forest insects, and brings together many useful references to new methods for the estimation of forest insect populations. Forest entomologists have found that the study of tree rings can give a picture of the history of insect outbreaks. The severest outbreaks which have caused the death of the standing trees can be traced in the age distribution of the trees which have grown up to replace them. This otherwise good paper is marred by the number of typographical errors, which are commendably few in the rest of the volume.

The paper by Dr W. R. Thompson entitled 'the fundamental theory of natural and biological control' does not seek to cover all the recent literature—only eight of the twenty-seven references are to post-war publications—because a number of general reviews are already available. Instead the essay is concerned mainly with comparing the views expressed by A. J. Nicholson (Outline of the dynamics of animal populations. *Aust. J. Zool.* **2**, 1-65: 1954) and those expressed earlier by Thompson himself. There is agreement on a number of fundamental issues, but whereas Nicholson maintains that populations are self-governing systems, Thompson thinks that they 'are not truly regulated but merely vary, although indefinite increase is unlikely and in the long run will become impossible'. 'If an organism does not multiply without limit this is because it is restricted by its intrinsic specific limitations' (p. 401). Many will welcome this clear restatement of Thompson's views in relation to those of Nicholson.

In addition to these papers on strictly ecological topics there are useful articles on insect behaviour, diapause, geographical variation, and the stability of scientific names which ecologists may well find useful. Lipke and Fraenkel's article on insect nutrition discusses not only the special requirements of insects' diet for vitamins, aminoacids and so on, but has a very interesting section on the host selection of plant feeding insects. The fundamental nutrients in plants are similar, but these authors argue that different plants have evolved mechanisms for the production and storage of peculiar glucosides, tannins, saponins, alkaloids and oils which make them unpalatable. Concomitantly

certain insect species have evolved tolerance or resistance to these substances, and even come to use them as attractants to the food to which they have become adapted.

The second volume of the *Annual Review of Entomology* is to appear in 1957, and ecologists will be glad to know that it will contain papers on Dynamics of Insect Populations by Dr M. E. Solomon, on Insects and Climate by Dr W. G. Wellington, and on Insect Migration by Dr C. B. Williams.

This new annual is likely to become quite indispensable as it is already attracting contributions of the highest quality from specialists in many parts of the world. The book would be even more useful if the bibliographies gave the full titles of the papers cited.

G. C. VARLEY

TERRESTRIAL ECOLOGY

W. Tischler (1955). *Synökologie der Landtiere.* Pp. xvi+415; 116 text-figures. Stuttgart: Fischer. Price DM 36.00.

It is often said that scientific disciplines are distinguished from one another more by their approach than by their subject-matter: by this criterion one is often tempted to regard 'ecology' as at least two separate subjects, according to whether it is studied in continental Europe or in the English-speaking countries. Tischler's book is outstanding in that it goes a long way towards bridging the gap between these two subjects owing to the author's evident familiarity with both. Even in the bibliography of some 1300 references, approximately equal numbers of German and English language sources are quoted and throughout the first part of the book, particularly, the same balance is preserved.

By restricting the field to terrestrial animals and habitats for its examples and for consideration in the 'special part' Tischler has been able in 400 pages to cover an impressive amount of ground and to match a very logical plan with numerous well-chosen examples. The first half of the book, in traditional style, is concerned with principles and successfully welds together subjects such as population fluctuations and succession on the one hand, biocenotic classifications, life-forms and the ecology of man-made habitats on the other, and reveals an immense amount of common ground in a treatment of topics such as matter and energy in the ecosystem, the ecosystem as a space-time structure and the structure of communities. It was in the latter group of chapters, in particular, that one reader at least found the juxtaposition of ideas from both kinds of ecology particularly stimulating. For instance, in a discussion of succession we find Lack's data on birds, Larsen's on Danish sand-dune beetles and Penth's on Heteroptera following one another, and we can readily appreciate the differences and similarities which result from change of scale and biology on the pattern of succession. Throughout this half of the book the accent is on synecological work, one of the precepts enunciated at the beginning and strictly adhered to being that it is not enough to study the single species and its immediate environment if its ecology is to be understood.

The second half of the book treats each of eight main climatically determined vegetation types in turn: shore, rain forest, deciduous forest, tundra, conifer forest, desert, steppe, and bush, and their variants. The discussion follows a uniform but not rigid plan under such headings as: living conditions, structure, food, biotic relationships, and over-wintering. These chapters are followed by a section on land types which result from human activity (buildings, gardens, ruins, arable and pasture fields, and hedges) which is the special interest of the Kiel ecologists. The section is a useful survey of

many papers in this important field, and shows that the work is distinguished by a combination of first class natural history observation on habits and life histories with a quantitative approach which, while not perhaps satisfying the more statistically minded worker, nevertheless seems to provide conclusions of biological significance. The final chapter is an appeal for enlightened land management and nature conservation. Owing to the large field covered in this part of the book theoretical discussion is at a minimum and some of the principles put forward in the first half seem to have scant application; this, however, reflects on ecological research as it is today rather than on this book, and an impressive range of literature is condensed in a most useful form.

The book is frankly a textbook and source of information; for this reason, perhaps, the treatment is mainly terse and impersonal, more controversial topics being either avoided or briefly mentioned by quoting references on both sides. For English readers, for instance, some expression of opinion on the merits of continental methods of community classification and analysis by the trellis diagram and other means would have been welcome; but Tischler remains impartial with a brief remark to the effect that the value of a method depends on its usefulness. Controversial matters in the field of population dynamics are mainly avoided but sometimes reported as though they were generally accepted. Two features stand out as being particularly useful for the student; firstly, there is a quite exceptional lack of jargon; generally used German technical terms are always explained when first introduced and also in a glossary, and are usually placed in brackets and accompanied by a more usual word when they appear in the text. Secondly, there are a large number of text-figures drawn by Tischler in order to summarize the data of other authors; these are mostly clear and easily understood although they sometimes express in black and white things which were stated originally with some caution, so that author's conclusions are made more positive than they might have chosen. There are many rather formidable 'food web' diagrams which, while they are admittedly useful condensations of scattered data are open to the criticism that, without quantitative data it is impossible to distinguish the important from the chance relationship; this too, however, is more of a reflection on ecology as it stands today than on the book under review.

To readers in this country Tischler's book could be of immense value as an introduction to Continental work on animal ecology, especially as practised in the German-speaking countries. It is also of great interest as a balanced appraisal of English and American work and the way it fits into a broader background, as seen by one who is particularly concerned with the practical approach mainly prevalent in present-day Germany.

A. MACFADYEN

RADIOCHEMICALS

Proceedings of the International Conference on the Peaceful Uses of Atomic Energy. Vol. 12. *Radioactive Isotopes and Ionizing Radiations in Agriculture, Physiology, and Biochemistry.* Pp. ix+553; numerous text-figs. New York: United Nations (London: H.M.S.O.) 1956. Price 63*s*.

Containing as it does more than 100 papers by nearly as many authors, this large volume is impossible to review in detail, if only because the quality of the different contributions varies almost as much as the subject-matter. The papers are nearly all surveys of recent work in fields varying in size over a wide range from the first on 'Radioisotopes in Biology and Agriculture' to specialized contributions such as 'Absorption of sulfur-35 by peanuts' or 'Distribution of $C^{14}O_2$ in liver glycogen'. There is little which is primarily

ecological, though a number of the papers read at the session on 'Tracer Studies in Agriculture' have clear ecological implications. The book is a useful source of information, especially because it brings together work done in many countries and makes available accounts in English of recent work in Russia and Japan which would otherwise be less easily accessible.

The volume is well produced and better bound that these things sometimes are. The advantage of the large double-column quarto format in allowing lavish treatment of tables would not seem to outweigh the disadvantages of a book which does not fit conveniently into an ordinary shelf, particularly as the possibility of large illustrations does not seem to have been exploited. From the bibliographic point of view the addition of an editor's name might have made the book easier to refer to and to catalogue—but these are minor criticisms of a valuable compilation.

H. C. GILSON

FRESH WATERS

Robert E. Coker (1954). *Streams, Lakes, Ponds.* Pp. xviii+327; 25 plates; 28 text-figures. Chapel Hill: University of North Carolina Press; London: Cumberlege. Price 48*s*.

The first ninety pages are devoted to the physical and chemical properties of water and during the course of them the conventional scheme of lake classification is mentioned. Three chapters are about running water. Remarks on streams are of a general nature and not everyone will agree with all of them; there is for example a strong school in Europe that hotly denies any connection between streamlined form and existence in running water. Several pages and seven text-figures are devoted to the animals and plants of streams and here a disadvantage from which the most excellent American book of this type must suffer becomes apparent—the fauna of America and of Europe is not the same. Any reader who, with the book open at Fig. 7, goes searching European streams for a water-penny will be disappointed, and indeed how many experts this side of the Atlantic could put a generic name to that extremely characteristic creature or even comment on its relationship to the sand-dollar? The other disadvantage outside the control of American authors is the unfavourable exchange rate which results in rather a high price. A chapter on rivers and another on pollution complete the running water section. Still water is dealt with more fully and after a general discussion there is a page or two on each phylum and on each order of insects.

A good deal of the information up to this point is at second or third hand and inevitably errors have crept in. The statement on p. 87 that *Prymnesium parvum* does not harm fish, quoted on the authority of another textbook, is not in accord with what Israelis have written in original works. However, the only type of reviewer who will fling critical stones of this kind without inhibition is the one who has never written a book himself and never intends to.

The last forty pages of the book, which are about fishponds, are the most interesting. This is a field in which Americans, working with a less severely commercial aim than Europeans, have made a unique contribution, and it is also one in which the author appears to have first-hand interest. Moreover anyone writing of ponds brought into existence only to produce a good crop of fish has a unifying theme which is bound to be lacking in a general treatment of the whole sphere of freshwater biology.

In short there is not a great deal here that is new either in the presentation or the ideas. The author, however, did not intend that there should be. He has written for 'the general reader as well as those with specialized interests' among whom he includes 'the student, the conservationist, the fish culturist, the sanitarian, the scientific agriculturist, the

engineer and the industrialist'. Such people will find in the book a simple, clear and straightforward account of what is known about freshwater and the animals that inhabit it.

T. T. MACAN

MARINE NATURAL HISTORY

Gianni Roghi & Francesco Baschieri (1956). *Dahlak* (translated by Priscilla Hastings). Pp. 280; 51 colour and monochrome photographs; 1 map and 2 diagrams. London: Kaye. Price 25*s*.

This is a popular account of an Italian expedition to study by means of diving equipment the sublittoral fauna of an island in the Red Sea off Massawa. The tone is set by the list of those taking part, which divides them into a 'scientific group' and a 'sports group'. They swam about with aqualungs and speared fish when they could, but apart from a few casual observations on their habits there is nothing scientific and certainly nothing ecological in the book.

The translation too is surprisingly poor and frequently brings one up short with an un-English phrase. Some of the under-water photographs are fairly good, but the book contains nothing outstanding.

H. C. GILSON

THE DYNAMIC CYCLE OF PLANKTON PRODUCTION

D. H. Cushing (1955). Production and a pelagic fishery. *Fish. Invest.* (II) **18**, No. 7. Pp. vi+106. Price 12*s*. 6*d*.

Fishery biologists have naturally long been prominent among those ecologists interested in investigating the quantitative aspects of food chains and the dynamics of 'production'. This paper is an investigation of the dynamic cycle that is the basis for a drifter fishery for herring in an area of the North Sea off the Northumberland coast. During the early summer the area supports several patches of plankton production and these were sampled on a 'grid' system of stations during a series of research vessel cruises in the spring and summer of 1949. Water samples and net samples of phytoplankton and zooplankton were taken, analysed in some detail and then used to construct contour maps of abundance. The paper presents some useful data on sampling methods and their accuracy and on the use of a flowmeter in a Hensen net. It is claimed that most of the significant plant production is in the form of diatoms, and the number of divisions made by the diatoms is calculated from observations on cell wall thickness and the decrease in their size. This is superficially an attractive method and the results it yields might be so valuable that it deserves thorough investigation. The data from culture experiments, etc. that are given are not adequate, however, to justify the confidence placed in the method, especially when the structure of diatoms and their behaviour in division and in culture is known to be so complex and when the method suggests division rates of up to three per day.

The data for *Calanus*, the most important zooplanktont, are interesting as an attempt is made to estimate mortality rates on the basis of the numbers of successive stages found on each cruise. The identification of at least one 'patch' of plankton through successive cruises is an interesting and valuable contribution. It is a pity that effort could not have been concentrated on to sampling this one patch more thoroughly once it had been observed. It is estimated that 90% of the production of the diatoms is eaten by *Calanus* and other zooplanktonts (though Table XXXII gives 99%) and that the herring make

serious inroads into the population of *Calanus*, especially in copepodite stages IV and V. Part of the paper is concerned with the problems of aggregation, both of herring shoals on to *Calanus* patches and of drifters on to herring shoals. These are examined by means of data from plankton samples, echo-surveys and catch statistics, but these data and the diagrams based on them do not provide an easily followed or convincing story. It is a pity that the quantitative aspects of the food chain could not have been followed through the zooplankton on to the herring and then the drifter fishery; this would have been more relevant to the main theme of the paper.

Although in many places the author stresses the value of considering the whole food chain, the quantitative results obtained in the various sections are nowhere, in fact, linked together. As a whole the paper is not easy to read and shows signs of careless editing (e.g. are not the labels of the abscissa and ordinates in Fig. 24 interposed?). The author deserves full credit for boldly attempting so comprehensive a study and for presenting several stimulating ideas. It is therefore unfortunate that his data and their analysis and presentation do not really quite stand up to the demands made upon them by the main thesis and some of the conclusions.

E. D. LE CREN

BOOKS RECEIVED

Procedure in Taxonomy. By Ed. T. Schenk and John H. McMasters. 3rd ed. enlarged and in part re-written by A. Myra Keen and S. W. Muller. Stanford University Press; London: Oxford University Press. 1957. Price 28*s*.

Key-List of the Palaearctic and Oriental Passerine Birds. By Owen E. Wynne. Arbroath: Buncle. 1956. Price 15*s*. 6*d*.

Key to the names of British fishes, mammals, amphibians and reptiles. By R. D. Macleod. London: Pitman. 1956. Price 12*s*. 6*d*.

Zoologie und das neue Bild des Menschen. By Adolf Portmann. Hamburg: Rowolt. 1956. Price DM 1.90.

The first fifty years. A history of the Kettering and District Naturalists' Society and Field Club. Kettering. 1956. No price given.

Selected Scientific Papers from the Istituto Superiore di Sanita. Vol. 1, No. 1 (in English). Oxford: Blackwell. 1956. Price 57*s*. 6*d*.

Adventure of the Sea. By James Fisher. London: Rathbone. 1956. Price 15*s*.

The Rabbit. By Harry V. Thompson and Alastair N. Worden. London: Collins. 1956. Price 16*s*.

ABSTRACTS

The abstracts are edited by Professor L. A. Harvey with the assistance in selecting and abstracting of J. A. Allen, J. D. Brayshaw, G. I. Crawford, T. A. W. Davis, A. E. Ellis, P. D. Gabbutt, N. A. Holme, S. J. Holt, D. Leatherdale, A. Macfadyen, C. Matheson, E. J. Moynahan, Miss E. Nelmes, W. R. Pickering, J. L. Cloudsley-Thompson, G. G. Vickers, Mrs M. Vincent, M. Williamson and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Professor L. A. Harvey, The University, Exeter.**

Separate copies of the abstracts suitable for mounting on cards can be obtained from **Blackwell Scientific Publications Ltd., 24-25 Broad Street, Oxford,** or through any bookseller; price 5*s.* 6*d.* per annum, post free (issued in May and November). Back numbers of the 'Notices of publications . . .' from Vol. 3 (1934) to Vol. 20 (1951) may also be had at 2*s.* for each annual set of two parts.

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Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above journal and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Balmain, K. H. & Shearer, W. M. (1956). Records of salmon and seatrout caught at sea. *Freshw. Salm. Fish. Res.* **11**, 1-12.

A survey of records of sea captures of salmon and sea trout between 1888 and 1954 and 1927 and 1954 respectively, with some undated records. Each species is mapped and it is emphasized how little is known of the sea lives of these fishes.

Barnes, H. & Barnes, M. (1954). The general biology of *Balanus balanus* L. da Costa. *Oikos*, **5**, 63-76.

An account of the growth-rate and reproductive cycle in this barnacle.

Cushing, D. H., Burd, A. C. 1956). Recruitment and maturity of the east-anglian herring. *Nature, Lond.* **178**, 86-87.

Evidence suggests that in 1952 the recruits comprised virtually the whole class of three-year olds. This is confirmed using Hodgson's method of identifying herring groups. These changes in the age distribution may be correlated with changes in the density of *Calanus*.

Dahl, E. (1956). Ecological salinity boundaries in poikilohaline waters. *Oikos*. **7**, 1-21.

Reviews transitional conditions from marine to brackish to fresh water using primarily the Baltic Sea but also other examples in the literature. Suggests that stable fresh and marine waters be labelled homoiohaline and unstable brackish and estuarine waters dependent on the sea for salinity, poikilohaline. Subdivides poikilohaline habitats into meta-, poly-, meso- and oligo-haline on the basis of faunistic changes, and relates these to degrees of salinity.

Jones, E. W. Knight- & Jones, W. C. 1956 . The fauna of rocks at various depths off Bardsey. I. Sponges, coelenterates and bryozoans. *Rep. Bardsey Bird Field Obs.* **1955**, 23-30.

A survey made by aqualung of the fauna of rocks at depths of 15, 25 and 35 metres off this Caernarvonshire island.

Keynes, R. D. (1956). The generation of electricity by fishes. *Endeavour*, **15** (60), 215-222.

Historical review and account of recent anatomical and physiological studies and theories as to function and evolutionary significance of phenomenon.

Lockley, R. M. (1956). The outermost rocks of Wales. *Nature in Wales*, **2**, 257-266.

Discusses the history, geology, botany, birds, insects and marine mammals of the Smalls, the Hats and the Barrels Reefs in St. George's Channel.

Perkins, E. J. (1956). The fauna of a sand-bank in the mouth of the Dee estuary. *Ann. Mag. Nat. Hist.* (12) **9**, 112-128.

Quantitative collections of the macrofauna along traverses at half-tide level in fine sand. Occurrence and density of the species is related to soil drainage.

Pyefinch, K. A. (1955). A review of the literature on the biology of the Atlantic salmon (*Salmo salar* Linn.). *Freshw. Salm. Fish. Res.* **9**, 1-24.

A valuable summary of the biology and migrations of the Atlantic salmon and of methods of investigation, with a comprehensive bibliography.

Savory, T. H. (1956). Sea-spiders. *Discovery*, **17**, 233-235.

A brief, popular account of the Pycnogonida, with notes on their classification and mention of five British species.

Venables, U. M. & Venables, L. S. V. 1955 . Observations on a breeding colony of the seal *Phoca vitulina* in Shetland. *Proc. Zool. Soc. Lond.* **125**, 521-532.

A general biological account especially concerning breeding.

(*b*) Fresh Water

Brook, A. J. (1956). Some botanical problems of freshwater fisheries research. *Proc. Linn. Soc. Lond.* **167,** 71-73.

Changes in phytoplankton populations after adding superphosphate to a trout loch.

Chandler, A. (1954). Causes of variation in the haemoglobin content of *Daphnia* (Crustacea: Cladocera) in nature. *Proc. Zool. Soc. Lond.* **124,** 625-630.

Variation with oxygen content, season and species is demonstrated.

Corbet, P. S. (1956). The influence of temperature on diapause development in the dragonfly *Lestes sponsa* (Hansemann) (Odonata: Lestidae). *Proc. R. Ent. Soc. Lond.* (A) **31,** 45-48.

Describes an obligate diapause in the egg with the optimum temperature for diapause development lying near to 10° C.

Fenwick, M. J. (1956). A comparative biology of *Asellus, Eucrangonyx* and *Gammarus*. *Ann. Rep. Oundle School Nat. Hist. Soc.* **1955,** 41-50.

Asellus is most often found in deep, almost stagnant water among plant debris; it tolerates low oxygen concentration, and any temperature from 0° to 30° C.

Gammarus favours shallow, fairly fast water, usually with a sandy bottom; it only survives in water of a very high oxygen concentration and in temperatures between about 10° and 20° C.

Eucrangonyx favours deep, shaded, almost stagnant ponds and pits; it survives in almost any oxygen concentration and in temperatures between 5° and 25° C.

Green J. (1956). Growth, size and reproduction in *Daphnia* (Crustacea: Cladocera). *Proc. Zool. Soc. Lond.* **126,** 173-204.

In a field and laboratory study the extrinsic and intrinsic factors are analysed; Lack's (1954) thesis that size and number of eggs is anticipatory of food supply is refuted.

Holden, A. V. (1956). Observations on the addition of chemical nutrients to small lakes. *Proc. Linn. Soc. Lond.* **167,** 68-71.

Rates of disappearance of phosphates and calcium in trout lochs.

Hynes, H. B. N. (1955). Distribution of some freshwater Amphipoda in Britain. *Verh. int. Ver. Limnol.* **12,** 620-628.

Describes and maps the distribution of the five British freshwater species of Gammaridae and discusses their ecological and interspecific relationships.

Khan, K. A. Nawaz. (1952). Brown trout of Kagan Valley. *Empire For. Rev.* **31,** 204-203.

A short account of stocking an Indian river. Contains observations such as that trout lie in pools where a spring-fed sidestream keeps the temperature at optimum level.

Moon, H. P. (1956). Observations on a small portion of a drying chalk stream. *Proc. Zool. Soc. Lond.* **126,** 327-333.

Owing to the reservoir formed by underground water storage capacity the stream dries slowly. The ecological and evolutionary significance of this situation is discussed in relation to a fauna of flies, beetles and a worm.

Nall, G. H. (1955). Movements of salmon and sea trout, chiefly kelts, and of brown trout tagged in the Tweed between January and May, 1937 and 1938. *Freshw. Salm. Fish. Res.* **10,** 1-19.

Returns of tagged fish, some of them recaught many times, indicated marked to and fro movements of both clean salmon and kelts, rather than a straight run either upstream or down to sea. The much larger numbers of sea trout showed an even greater restlessness, but brown trout were more sedentary.

Pyefinch, K. A. (1956). The Brown Trout Research Laboratory. *Proc. Linn. Soc. Lond.* **167,** 67-68.

A general account of the work of the laboratory. Introducing the papers by Holden, Brook and Stuart.

Stuart, T. A. (1956). The selection of spawning sites by trout. *Proc. Linn. Soc. Lond.* **167,** 74-76.

On suitable gravel banks the water flows directly downwards into the gravel, and the fish detect this while swimming. Gravels can be altered artificially to produce this flow.

Thomasson, K. (1956). Reflections on arctic and alpine lakes. *Oikos,* **7,** 117-143.

A broad review of conditions in arctic and alpine lakes throughout the world, discussing heat economy, ultra-violet radiation, nutrient supply and their influence on the composition of the plankton.

(*c*) Land

Allen, P. (1956). Observations on the biology of some Agromyzidae (Diptera). *Proc. R. Ent. Soc. Lond.* (A) **31,** 117-131.

A study of thirteen species of Agromyzidae with information on their host plants, period of occurrence and parasites with additional studies, on some species, of the length of the stadia, and mortality.

Anon. (1956). Breeding of shags on Lundy 1954-55. *9th Ann. Rep. Lundy Field Soc.,* 28-31.

180 nests were found on the island, which is in the Bristol Channel, in the two years, showing far the most frequent clutch-size to be 3, but tailing off to 1 and 6. Hatching success was 13·9%, and fledgling success 93·6% of eggs hatched. Nests under rocks were more successful than nests in the open, and nests in which the first egg hatched before the end of May reared an average of 1·09 more young than nests in which the first egg hatched after mid-June.

Anon. (1954). The pine looper moth. *Scot. For.* **8,** 32, 174.

Two outbreaks of *Bupalus piniarius* in Cannock Chase and Culbin Forest, Morayshire, respectively.

Anon. (1953). War on the grey squirrel. *Quart. J. For.* **47,** 155-156.

Gives a map showing distribution; districts seriously infected are: south and south-east England, the Chilterns and the Welsh borders.

Anon. (1955). Putting down the grey squirrel. *Quart. J. For.* **49,** 291-295.

Results during the first two years of the 'shilling-a-tail' campaign. Particulars of two improved cage traps.

Anon. (1955). Myxamatosis in hares. *Quart. J. For.* **49,** 141.

The first definitely confirmed case of a hare (*Lepus timidus*, the blue hare) dying of myxomatosis in Great Britain (Northern Ireland).

Armour, C. J. & Thompson, H. V. (1955). Spread of myxomatosis in the first outbreak in Great Britain. *Ann. Appl. Biol.* **43,** 511-518.

The first outbreak of myxomatosis in Britain amongst rabbits was at Bough Beech, near Edenbridge, Kent, in October 1953. The spread of the disease is considered, as also are the role of insect vectors, rabbit immunity and after-effects on rabbit populations.

Axell, H. E. (1956). Predation and protection at Dungeness bird reserve. *Brit. Birds,* **49,** 193-212.

Herring gulls, black-headed gulls, and common terns bred successfully on shingle till 1939, but in the absence of protection during and after the war they became depleted by human interference and an increase of natural predators. Prolonged persecution led to lack of vitality in the herring gull colony. The steps taken to reduce the losses from predators since protection was resumed in 1952 are described.

Banks, C. J. (1956). Observations on the behaviour and mortality in Coccinellidae before dispersal from the egg shells. *Proc. R. Ent. Soc. Lond.* (A) **31,** 56-60.

Important causes of mortality in the egg stages of *Coccinella 7-punctata, Adalia 2-punctata* and *Propylea 14-punctata* were infertility and predation by newly hatched larvae of the same batch. Infertile eggs were only common in *C. 7-punctata* and these were always eaten by young larvae. The extent of predation appears to be associated with the size of the egg batch, in all three species. Experiments show that larval life is doubled by the provision of one coccinellid egg.

Bentley, E. W., Bathard, A. H. & Hammond, L. E. (1955). Some observations on a rat population in a sewer. *Ann. Appl. Biol.* **43,** 485-494.

A study of populations of *Rattus norvegicus* in a London sewer, and of the effects of poisoning. Factors influencing population size are briefly considered, and their specificity for a given type of sewer emphasized.

Beven, G. (1956). Further observations on the bird population of an oakwood in Surrey (Eastern Wood, Bookham Common)—II. Including some comparisons with scrub and farmland. *Lond. Nat.* **35** (1955), 21-32.

Fluctuations in numbers of territories of robins and wrens over nine years and in the numbers of birds throughout the year are discussed with reference to climate and vegetational changes; some robins and possibly some wrens leave the wood in winter. Numbers of tits throughout the year are discussed with reference to flocking; some *Parus* spp. leave the wood in winter, but long-tailed tits, which breed in the grassy plains, are numerous in the wood then. Numbers of willow warblers declined by more than half during 1950-55. Chaffinches breed in the wood and on the grassy plains, but leave both in late summer and autumn; they are numerous on adjoining farmland in winter. Wood pigeons rest in the wood during winter, but feed on the farmland. (Cf. 1953, *Lond. Nat.* **32** (1952), 51-77; 1954, *J. Anim. Ecol.* **23,** 187.)

Bishop, D. (1955). The emergence of larvae of *Heterodera rostochiensis* under conditions of constant and of alternating temperature. *Ann. Appl. Biol.* **43,** 525-532.

Potato-root eelworm larvae emerged from cysts in increased numbers when the temperature was alternated between 25 and 15° C in the presence of a hatching stimulant.

Boyd, J. M. (1956). The sheep population of Hirta, St. Kilda, 1955. *Scot. Nat.* **68,** 10-13.

The population has both decreased and become tamer since 1952.

Boyd, J. M. (1956). Fluctuations of common snipe, jack snipe and golden plover in Tiree, Argyllshire. *Bird Study,* **3,** 105-118.

Analysis of game records of the Tiree estate over 25 years, including unbroken records between 1929 to 1939 and 1945 to 1954, provides evidence of annual and monthly fluctuations over the shooting season. Correlated review of weather conditions during the migratory season throws some light on the influence of wind direction on movement into the island.

Boyd, J. M. (1956). The St. Kilda field mouse (*Apodemus sylvaticus hirtensis* Barrett-Hamilton), population in the village area, Hirta, May 1955. *Oikos,* **7,** 110-116.

Longworth trapping at five stations in May 1955. 33 mice caught, total catch with retrapping 54 for 100 trap nights. Comparison with Harrisson and Moy Thomas's observations in 1931 shows a greater population with more diurnal activity. Range of and average weights of males and females stated; sex ratio 1·6 males to 1 female.

Broadhead, E. & Thornton, I. W. B. (1955). An ecological study of three closely related psocid species. *Oikos,* **6,** 1-50.

The geographical and ecological distributions of *Elipsocus melachlani*, *E. westwoodi* and *E. hyalinus* in the Malham Tarn area. Laboratory observations are used in analyses of food habits, reproductive behaviour and sex ratios. Micro-climatic conditions of the habitats are analysed by means of a thermistor for temperature and Solomon papers for humidity.

Broekhuysen, G. J. (1956). Moult adaptation in relation to long-distance migration. *Nature, Lond.* **178,** 489-490.

General body, wing and tail moulting occurs together in *Hirundo rustica* and *Delichon urbica*, and there is no delay in moult of flight feathers as in *Puffinus tenuirostris*. Apparently this adaptation is lacking in *H. rustica* and *Delichon urbica*.

Brown, L. E. (1956). Field experiments on the activity of the small mammals, *Apodemus*, *Clethrionomys* and *Microtus*. *Proc. Zool. Soc. Lond.* **126,** 549-564.

Trapping and laboratory information revealed alternation of activity between species. Discussion of Miller's (1955) paper and the differences between laboratory and field experiments.

Brown, P. W., Allan, R. M. & Shanks, P. L. (1956). Rabbits and myxomatosis in the north east of Scotland. *Scot. Agric.* **35,** 204-207.

Outlines the increase in N.E. Scotland from the early nineteenth century, and the rapid decline after the introduction of myxomatosis in Kincardineshire in 1954. A flying insect, possibly *Simulium reptans,* was probably responsible for the spread of the disease in 1955.

Browne, K. & Browne, E. (1956). An analysis of the weights of birds trapped on Skokholm. *Brit. Birds,* **49,** 241-257.

Over 4000 birds of 69 species were weighed 1947-53. Migrants weigh less in spring than in autumn.

Bullock, T. H. (1955). Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.* **30,** 311-342.

A wide survey of problems of adaptation and its incidence; completely different types of behaviour exist in related forms but in general 'nature has learned so to exploit the biochemical situation as to escape from the tyranny of a single application of the Arrhenius equation' (Barcroft 1934).

Church, H. F. (1956). The mute swan population of the eastern Borders. *Bird Study,* **3,** 212-217.

Monthly distributional counts of mute swans in the lower Tweed valley and on adjoining coast flats from 1952 to 1956 show regular seasonal movements between estuary in summer to coast in winter. The summer estuarine population is of non-breeding birds.

Collyer, E. (1955). Some predacious insects of fruit trees: capsid bugs. *Rep. East Malling Res. Stn.* (A) **38,** 155-159.

Descriptions of some predacious capsid bugs found on fruit trees, with notes on their life-history and occurrence.

Cotterell, R. (1954). Grey squirrel destruction. *Quart. J. For.* **48,** 104-108.

Details the measures taken on an estate at Garnons, Herefordshire, and describes the progress made. Reprinted from 'Three against the grey squirrel', *Field,* 7 Jan. 1954.

Coulson, J. C. (1956). Mortality and egg production of the meadow pipit with special reference to altitude. *Bird Study,* **3,** 119-132.

Analysis of B.T.O. nest record cards, ringing recoveries and diaries of A. Whitaker and F. C. R. Jourdain. Breeding is related to latitude and altitude, being later in the north and at higher altitudes. Clutch size is also smaller at higher altitudes but not, in Britain, at lower latitudes. Incubation and fledging periods are given, general hatching success 54 %, fledging success 80 %, hence breeding success 43 %, but increasing at higher altitudes, possibly because of lower predation pressure. Mortality rates are estimated for 1st year and for adults.

Cragg, J. B. & Hobart, J. (1955). A study of a field population of the blowflies *Lucilia caesar* (L.) and *L. sericata* (Mg.). *Ann. Appl. Biol.* **43,** 645-663.

The dispersion, population density and longevity of blowflies on coastal farm land in Caernarvonshire.

Crooke, M. (1954). The pine looper moth. *Quart. J. For.* **48,** 36-38.

An outbreak in Cannock Chase, Staffordshire, the first serious outbreak in Britain in recent history. Life cycle.

Crooke, M. & Kirkland, R. C. (1956). The gale of 1953: an appraisal of its influence on forest pest populations in pine areas. *Scot. For.* **10,** 135-145.

Mainly concerns the bark beetles *Myelophilus piniperda* and *Hylastes ater* and the weevil *Hylobius abietis,* continuing a report elsewhere on 1953-54. Deals with population changes, parasitism and general ecology.

Davis, R. A. (1956). Rats and mice: their natural history and economic importance. *Discovery,* **17,** 115-121.

A popular article on the pest and public health status of rats and mice.

Duffy, E. A. J. 1956. Recent observations on infestation of an unusual type of ambrosia 'pinhole borer' beetle damage in wawa *Triplochiton scleroxylon*. *Empire For. Rev.* **35**, 198-200.

A platypodid beetle *Sommerius tuberculatus* attacks wawa in west Africa. The galleries are lined with a thick deposit of fungus 'ambrosia' and confined to the heartwood. A somewhat similar state occurs with the borehole borer of teak *Diamantus arcuatus*.

Dundee, Earl of 1956. Rabbit clearance. *Scot. For.* **10**, 12-14.

Costs and methods of completing rabbit clearance after an outbreak of myxomatosis.

Ellenby, C. 1956. The cyst of the potato-root eelworm *Heterodera rostochiensis* Wollenweber as a hatching unit. *Ann. Appl. Biol.* **44**, 1-15.

Larval emergence from halved cysts of the potato-root eelworm was greater than from intact cysts and the emergence rate was enhanced further when halved cysts were treated with trypsin. There is some doubt whether trypsin affects the cyst wall or the egg shell. Free eggs probably hatch more efficiently than eggs in cysts.

El-Ziady, S. & Kennedy, J. S. 1956. Beneficial effects of the common garden ant *Lasius niger* L., on the black bean aphid, *Aphis fabae* Scopoli. *Proc. R. Ent. Soc. Lond.* (A) **31**, 61-65.

Field and glasshouse experiments show that the ants afforded some protection to the aphids against their natural enemies. The ants increased the rate of aphid multiplication whether enemies were present or not, and delayed the production of winged forms.

Fisher, R. C. 1954. Some problems in forest-products entomology. *Rep. 9th Commonw. Ent. Conf. London*, pp. 117-122.

Somewhat generalised but a good short conspectus of the present position of research into pests of timber.

Gilbert, O. 1956. The natural histories of four species of *Calathus* (Coleoptera, Carabidae) living on sand dunes in Anglesey, North Wales. *Oikos*, **7**, 22-47.

Life histories of *Calathus erratus*, *C. fuscipes*, *C. melanocephalus* and *C. mollis* on coastal dunes in north Wales, using field observations, genitalia, egg production, and experiments in rearing each species in the laboratory. Pit-fall traps and artificial shelters are used in field estimations.

Goodey, J. B. 1956. The susceptibility of potato varieties to infestation by the eelworms *Ditylenchus destructor* and *D. dipsaci*. *Ann. Appl. Biol.* **44**, 16-24.

Twenty-five varieties of potato tuber were found to be susceptible to attack by potato-derived populations of the eelworm *Ditylenchus destructor*, whereas a race of the same species from mushroom spawn had almost no effect on potatoes. The degree of host preference was not so marked by *D. dipsaci*, although shoot tissue was attacked more readily than tubers.

Gorvett, H. 1956. Tegumental glands and terrestrial life in woodlice. *Proc. Zool. Soc. Lond.* **126**, 291-314.

The theory is convincingly presented that these glands serve as a defence mechanism against spiders.

Harris, W. V. 1955. Termites and forestry. *Empire For. Rev.* **34**, 160-166.

Biology, ecological results, natural resistance and timber impregnation.

Harrison, J. L. 1956. Some small mammals of Bookham Common. *Lond. Nat.* **35** (1955), 12-20.

The relative abundance of small mammals in damp oakwood, grass with scrub, an area transitional between them, and wet valley bottom assessed by means of traps in late 1955. The species captured, *Sorex araneus*, *Neomys fodiens*, *Clethrionomys glareolus*, *Microtus agrestis*, *Apodemus sylvaticus* and *Micromys minutus*, did not vary greatly in the four areas. More *A. sylvaticus* were caught in the wood than elsewhere. *C. glareolus* was significantly more numerous in the live than break-back traps. Owl pellets contained the remains of more voles and fewer shrews than were trapped, also four additional species. Includes a note on infestation of *Apodemus*, *Clethrionomys* and *Microtus* by the mite *Trombicula autumnalis*, a review of the factors affecting numbers of mammals caught in traps, a description of an inexpensive live trap, and a key to the 13 species likely to occur in the area.

Hussey, N. W. (1952). A contribution to the bionomics of the green spruce aphid (*Neomyzaphis abietina* Walker). *Scot. For.* **6**, 121-130.

A light-intolerant insect feeding on the lower sides of shaded shoots with a recorded rate of increase of 41% per day in the field. Life history, control and ecology.

Ingleby, J. A. (1956). Sheep, foxes and rabbits. *Scot. Agric.* **36**, 69-70.

Sheep flocks in Aberdeenshire have benefited by the disappearance of rabbits and have not suffered unduly from predators, despite the increased numbers and wider distribution of foxes.

Jones, F. G. W. (1956). Soil populations of beet eelworm (*Heterodera schachtii* Schm.) in relation to cropping. II. Microplot and field plot results. *Ann. Appl. Biol.* **44**, 25-56.

Microplots 2 ft 4 in. × 3 ft 4 in. delimited by concrete slabs and slotted corner posts used to surmount some of the difficulties encountered in the study of field populations of nematodes. Population effects of Cruciferae and Chenopodiaceae are discussed.

Jones, N. G. Blurton (1956). Census of breeding Canada geese 1953. *Bird Study* **3**, 153-170.

Data largely from B.T.O. census returns and from wildfowl counts. Relates with few exceptions to feral birds, the species being introduced from America at intervals since at least 1678. Detailed locality records listed, the total population being between 3600 and 3900. Discusses habitat, breeding, food, predation and movements. Concludes that the species has filled an unoccupied, grazing niche and is controlled by no natural predator. It is occasionally limited by mass egg destruction by humans.

Kisimoto, R. (1956). Effect of crowding during the larval period on the determination of the wing-form of an adult plant-hopper. *Nature, Lond.* **178**, 641-642.

Crowding is important in the determination of wing-form in *Nilaparvata lugens*. Low density is necessary for the occurrence of the brachypterous female. Optimal crowding accelerates the development of the larvae. Wilting of the host plant produces the macropterous form.

Laidlaw, W. B. R. (1952). Silvicultural causes and prevention of forest insect epidemics. *Quart. J. For.* **46**, 16-22.

The effects of different silvicultural systems on populations of insect pests. Systems are broadly grouped into natural and artificial woods and the latter into pure, even and uneven aged.

Laurence, B. R. 1956. On the life history of *Trichocera saltator* Harris (Diptera, Trichoceridae). *Proc. Zool. Soc. Lond.* **126**, 235-243.

The life history of a gnat whose larvae live in cow pats.

Leslie, P. H., Tenner, J. S., Vizoso, M. & Chitty, H. 1955. The longevity and fertility of the Orkney vole, *Microtus arvalensis* as observed in the laboratory. *Proc. Zool. Soc. Lond.* **125**, 115-125.

In a study of longevity and fertility statistics the life table, age specific fertility and mortality rates and intrinsic rate of increase are tabulated. It is shown that, owing to females producing fewer young and at a more advanced age, this species has a lower rate of increase and is longer lived than is *M. agrestis*.

Lockie, J. D. 1956. More light on myxomatosis. *Scot. Agric.* **36**, 44-45.

The effectiveness of rabbit fleas as vectors of the myxomatosis virus is shown by population kills reaching 95%. Each rabbit could harbour up to 27 fleas. Immunity is briefly considered; the presence of antibodies in surviving rabbits is rare.

London Natural History Society (1956). The survey of Bookham Common. Fourteenth Year. *Lond. Nat.* **35** (1955), 9-32.

Brief summaries of work in 1955 on grass-inhabiting Mantis, B. W. Graves, p. 11; bird populations, G. Beven, p. 11; and mammals, chiefly the status of rabbits, G. Beven and C. P. Castell, pp. 11-12. Also contains an account of the relative abundance of small mammals, J. L. Harrison, pp. 12-20, and further work on bird populations in woodland, rough grass and farmland, G. Beven, pp. 21-31).

Mackenzie, J. M. D. (1952). The encouragement of birds in commercial plantations by nest boxes and other means. *Scot. For.* **6,** 10-17.

Populations of hole-breeders, resident and migrant, and of treecreepers may be increased by the provision of nest sites. Other species can be increased by appropriate means, but are of less importance. Nest sites are thought to be the normal control, but after they are increased by boxes, the resultant populations are more vulnerable to other limiting factors.

Marshall, A. J. & Wilkinson, O. (1956). Reproduction in the Orkney vole (*Microtus orcadensis*), under a six-hour day-length and other conditions. *Proc. Zool. Soc. Lond.* **126,** 391-395.

Under a regime of abundant food and summer temperatures there is no significant effect of day length on breeding rate.

Massee, A. M. (1955). Problems arising from the use of insecticides: effect on balance of animal populations. *Rep. East Malling Res. Stn.* A **38,** 137-140.

The fluctuation in populations of four common pests in fruit orchards, and the effects of chemical spraying upon these populations. The need for spray chemists to collaborate with entomologists and to seek selective insecticides and fungicides is emphasized.

Miller, R. S. (1955). Activity rhythms in the wood mouse, *Apodemus sylvaticus* and the bank vole, *Clethrionomys glareolus*. *Proc. Zool. Soc. Lond.* **125,** 505-519.

The results of laboratory measurements are presented and theories concerning activity rhythms in small mammals are discussed. It is considered that differences in rhythmic behaviour of these two species are critical in relation to competition between them in the same localities.

Moreau, R. E. (1955). Ecological changes in the palearctic region since the Pliocene. *Proc. Zool. Soc. Lond.* **125,** 253-295.

A most important history of the climatic changes during the glacial periods written by a biologist for biologists; a bibliography of 200 references includes Russian and central European work.

Oakeley, R. P. Bagnall- (1956). The Egmere starling roost. *Norfolk Bird Rep.* **1955,** 17-23.

A winter roost in a six-acre larch plantation estimated to hold 3½ million birds, some coming from thirty miles away. Most of the birds were thought to be of Continental origin.

Owen, C. & Owen D. (1955). One effect of rabbits on downland vegetation. *Wilts. Arch. Nat. Hist. Mag.* **56,** 52-53.

Effect on the vegetation around the burrow, with a photograph.

P[arsons], A. G. (1956). The common buzzard and associated problems. *Rep. Cornwall Bird Watching Pres. Soc.* **25** (1955), 39-41.

Few pairs of buzzards bred in Cornwall in 1955, evidently owing to the virtual disappearance of rabbits. Buzzards seen near poultry yards were thought to have been more likely after rats and mice than poultry.

Prosser, C. L. 1955). Physiological variation in animals. *Biol. Rev.* **30,** 229-262.

A discussion of physiological variation from the evolutionary and species-formation point of view. Many examples of variation in ecological range are given.

Robson, R. W. (1956). The breeding of the dipper in north Westmorland. *Bird Study,* **3,** 170-180.

Data obtained by observation and by ringing and trapping. Colour rings relatively unsuccessful being difficult to see and wearing badly. Distribution, territories, nest sites, breeding and mortality are discussed.

Shorten, M. & Courtier, F. A. (1955). A population study of the grey squirrel *Sciurus carolinensis* in May 1954. *Ann. Appl. Biol.* **43,** 494-510.

A population of grey squirrels near Petersfield, Hampshire, was observed by means of trapping, marking and releasing for nine days. Aspects of particular interest are movement patterns, sex ratios and age ratios.

Snow, D. W. (1956). The annual mortality of the blue tit in different parts of its range. *Brit. Birds*, **49**, 174-177.

Annual mortality was estimated by the examination of museum specimens collected in the breeding season, first year birds being recognizable. In Britain the annual mortality of adults is about 70%. Mortality is higher in juveniles than in adults in October and November, thereafter about equal. The annual mortality of adults in different regions is correlated with clutch-size, e.g. in Britain the clutch is 11·6, and 30% of the population is adult, in the Canary Islands with the clutch 4·3, 55% of birds are adult.

Southern, H. N. (1956). Myxomatosis and the balance of nature. *Agriculture*, **63**, 10-13.

Disappearance of rabbits resulted in unusual activity by foxes, stoats and weasels which reduced mice and vole populations and consequently of owls. Buzzards ceased to breed. (Also reprinted in *Quart. J. For.* **50**, 1956, 303-307.)

Southwick, C. H. (1956). The abundance and distribution of harvest mice *Micromys minutus* in corn ricks near Oxford. *Proc. Zool. Soc. Lond.* **126**, 449-452.

An unusual abundance during the winter of 1954-55 is reported and the history of its appearance during this century is reviewed. A very patchy distribution in the district is revealed.

Spires, D. (1955). Aspects of the ecology of the house-sparrow. *Starfish*, **8**, 11-16.

Observations on autumn flocking, winter roosts, weather movements and breeding biology.

Tooke, F. G. C. (1955). The eucalyptus snout-beetle, *Gonipterus scutellatus* Gyll.; a study of its ecology and control by biological means. *Dept. Agric. Div. Ent. Pretoria*. Ent. Mem. **3**. Review by R. N. Chrystal. 1955. *Empire For. Rev.* **34**, 298-299.

Imported from Australia, where it was unimportant, the insect became a serious pest in S. Africa. A Mymarid parasite discovered in S.E. Australia, *Anaphoidea nitens*, was imported and proved almost a complete success. The parts played by site and climatic factors, and parasitic action are described.

Urquhart, B. (1952). Slugs and natural regeneration. *Quart. J. For.* **46**, 110-112.

Beech and sycamore one-year seedlings mainly were damaged. Results of poisoning.

Varty, I. W. (1953). *'Cinaropsis pilicornis'*: a rare aphid attacking spruce transplants. *Scot. For.* **7**, 86-87.

Life cycle and control.

Wallace, H. R. (1955). The influence of soil moisture on the emergence of larvae from cysts of the beet eelworm, *Heterodera schachtii* Schmidt. *Ann. Appl. Biol.* **43**, 477-484.

Effects of soil moisture and aeration on larval emergence from cysts. Emergence increased with oxygen concentration. Water-pressure trials suggest that the surface forces of a water film may inhibit larval migration from cysts.

Wallace, H. R. (1956). Soil aeration and the emergence of larvae from cysts of the beet eelworm, *Heterodera schachtii* Schm. *Ann. Appl. Biol.* **44**, 57-66.

Larval emergence from cysts of *H. schachtii* increases with aeration of the soil. Good soil tilth favours high rates of emergence.

White, M. G. (1954). The house longhorn beetle *Hylotrupes bajulus* L. (Col. Cerambycidae) in Great Britain. *Forestry*, **27**, 31-40.

Records of infestations since 1934 summarized according to locality and type, the most being from Surrey. Attack in buildings may be of long standing and extinct, or of more recent origin and usually active. Out of doors, living insects range from dead parts of a standing Douglas fir to sawn Scots pine. Active attack in packing-cases and crates of various origins has been recorded from different parts of the country.

Woodroffe, G. E. (1956). The Hemiptera-Heteroptera of an apple tree. *Ent. mon. Mag.* **92,** 35.

The Anthocorids and Mirids beaten from a neglected apple tree in Buckinghamshire in late July 1955 are listed and their relative abundance shown. The results are compared with the Heteropterous fauna generally present in fruit orchards in Kent.

Yapp, W. B. (1956). The birds of high-level woodlands. The breeding community. *Bird Study,* **3,** 191-204.

Lists twenty-four birds which breed in woods at 1000-1500 ft, discussing their relative occurrence in Britain and in relation to tree species. Woodland species which require shelter and a thick shrub layer are absent.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Anon. (1956). The amateur in science. *Endeavour,* **15** (59), 115-116.

Mentions role of amateurs in ecological work.

Bailey, N. T. J. (1956). On estimating the latent and infectious periods of measles. I. Families with two susceptibles only. *Biometrika,* **43,** 15-22.

Maximum likelihood scoring for estimating the chance of contracting the disease, the mean and variance of the latent period, and the length of the infectious period which is assumed to be constant. The estimates are based on the distribution of households with one and two cases and on the distribution of time between cases when two occur.

Bary, B. McK. (1956). The effect of electric fields on marine fishes. *Mar. Res. Edin.* **1,** 1-32.

Describes tank experiments, mostly on golden grey mullet, *Mugil auratus* Risso, using for the most part a pulse generator. Discusses relationships between fish length, voltage gradient in the water, pulse length and pulse frequency, and compares effects upon different species of fish.

Betts, M. M. (1956). Further experiments with an artificial nestling gape. *Brit. Birds,* **49,** 213-215.

A new method of using an artificial nestling gape to collect food samples demonstrates the inadequacy of observation when several items together are brought. (See also Betts, M. M., 1954, *Brit. Birds,* **47,** 229-231. Abstract in 1955, *J. Anim. Ecol.* **24,** 482.)

Chant, D. A. & Muir, R. C. (1955). A comparison of the imprint and brushing machine methods for estimating the numbers of the fruit tree red spider mite, *Metatetranychus ulmi* (Koch), on apple leaves. *Rep. East Malling Res. Stn.* (A) **38,** 141-145.

The brushing machine method appears to be the more efficient. Sample size should probably be increased in both cases.

Coulianos, C.-C. (1955). A new temperature gradient apparatus for insects especially for field work. *Oikos,* **6,** 71-77.

A long glass-walled trough with glass lid and a copper floor projecting into a can at each end, one can being filled with a freezing mixture the other with hot water. Methods of modifying relative humidity are discussed.

Ford, E. B. (1956). The study of organic evolution by observation and experiment. *Endeavour,* **15** (59), 149-152.

Reviews development of ecological and genetical methods which have made it possible in the last 40 years to study the process of evolution in natural populations.

Good, I. J. & Toulmin, G. H. (1956). The number of new species, and the increase in population coverage, when a sample is increased. *Biometrika* **43,** 45-63.

Using the smoothed distribution of the number of species represented 1, 2, . . . times in the original sample. The variance of the simple estimate becomes very large by the time the second sample is twice the first, but this can be overcome to some extent, allowing estimates of expectations in samples up to five times the original.

Goto, H. E. (1956). *Architomocerura* Denis, 1931 (Collemb., Isotomidae) an immature stage of *Tomocerus* Nicolet, 1841 (Collemb., Tomoceridae). *Ent. mon. Mag.* **92,** 49-51.

Includes a key for the separation of the first instars of *T. minor*, *T. longicornis* (=*A. litsteriana*) and *A. crassicauda.*

Groves, J. R. (1955). A comparison of bait and light traps for catching codling moths, *Cydia pomonella* L. *Rep. East Malling Res. Stn.* (A) **38,** 146-149.

Briefly discusses reasons for the differences in populations caught by the two types of trap.

Hewer, H. R. (1955). Notes on the marking of Atlantic seals in Pembrokeshire. *Proc. Zool. Soc. Lond.* **125,** 87-93.

A method for ring marking the foot is described ; information on distances covered by marked seals is given.

Hyatt, K. H. (1956). A collection of mites from stable manure. *Ent. mon. Mag.* **92,** 36-38.

Of the twelve mites collected from bullock dung and straw from a shed in southern England in early May, *Macrocheles merdarius*, *Digamasellus longiusculus*, *D. foveolatus*, *Prodinychus tuberosus* and *Leiodinychus pilosella* are recorded for the first time in the British Isles. The chaetotaxy of the dorsal shields of both sexes of the last species is described and figured.

Jónasson, P. M. (1955). The efficiency of sieving techniques for sampling freshwater bottom fauna. *Oikos,* **6,** 183-207.

Discuss the use of different grades of sieve mesh used interchangeably in a modified Ekman sampler. Shows that the commonly used 0·6 mm mesh passes many more species than has been recognized and calls for drastic revision of results published in the literature and also of sieving methods in future.

Kerrich, G. J. (1956). The Encyrtid genus *Homalotyloidea* Mercet in the British Isles with a description of the male (Hym., Chalcidoidea). *Ann. Mag. Nat. Hist.* (12) **9,** 106-107.

The known range of *H. dahlbomii* (Westwood) is now Tuscan Archipelago, Madrid district, Jersey, Kent, London district, Yorkshire and Portmarnock near Belfast.

Macfadyen, A. (1956). The use of a temperature integrator in the study of soil temperature. *Oikos,* **7,** 56-81.

Describes an apparatus using thermistors and silver voltameters for measuring mean temperatures over periods of the order of a week, and its field use in sampling at precise levels in soil. Discusses results in relation to ecological conditions at two sites, indicating degrees of accuracy and limitations.

Mould, R. C. L. (1955). Designing game coverts. *Quart. J. For.* **49,** 281-290.

The general principles for the design of game coverts to serve also as commercial woods.

Pickard, B. C. (1956). The distribution of *Omocestus rufipes* (Zett.) in Great Britain, with descriptions of the two British species of the genus *Omocestus* Bol. (Orth., Acrididae). *Ent. mon. Mag.* **92,** 51-52.

O. rufipes recorded from 26 counties of Great Britain, but records for Perthshire, Roxburghshire, Cumberland, Yorkshire, Lancashire, Cheshire and Caernarvonshire refer to brown males of *O. viridulus* form *rubiginosa* and *O. rufipes* is probably restricted to some 6-7 counties. Descriptions of both sexes of *O. viridulus* and *O. rufipes* and males of *O. viridulus* form *rubiginosa* are given, with notes on their habitats and stridulation.

Southwood, T. R. E. (1956). The structure of the eggs of the terrestrial Heteroptera and its relationship to the classification of the group. *Trans. R. Ent. Soc. Lond.* **108,** 163-221.

Includes a section devoted to a description of the structure, oviposition, development and the hatching of the eggs.

Taylor, L. R. (1955). The standardization of air-flow in insect suction traps. *Ann. Appl. Biol.* **43,** 390-408.

Variation of air-flow in five types of insect suction trap considered in relation to sample size. Traps with the filter cone enclosed in a cylinder and using axial-flow fans are most efficient. Expected errors are indicated.

Woodroffe, G. E. (1956). Some Hemiptera-Heteroptera from Virginia Water, Surrey, including *Pilophorus confusus* (Kb.) (Miridae) new to Britain. *Entomologist,* **89,** 84-87.

This account of the species found in an overgrown, shallow, sandy depression includes a key to the four British species of *Pilophorus,* three of which were present.

Yapp, W. B. (1956). The theory of bird transects. *Bird Study,* **3,** 93-104.

Presents a formula for determining the density of organisms in an area on the basis of the numbers encountered in a unit of time, the effective radius of the organism, its average speed and the speed of the observer. The method is more useful for comparative purposes than for absolute determinations.

3. PARASITES

Bailey, L. (1955). The epidemiology and control of *Nosema* disease of the honey-bee. *Ann. Appl. Biol.* **43,** 379-389.

The proportion of honey-bees infected by the protozoan parasite *Nosema apis* declines in summer, as old bees die and transmission to newly emerged bees ceases. Spores of *N. apis* survive the summer on contaminated comb, and although only a few bees may become infected in the autumn they spread the disease when they join the winter cluster. Control measures are discussed.

Griffiths, G. C. D. (1956). Host records of Dacnusini (Hym., Braconidae) from leaf-mining Diptera. *Ent. mon. Mag.* **92,** 25-30.

A list of parasites, with hosts, localities and dates, and one of hosts, with the parasite species reared from them.

Wright, C. A. (1955). Studies on the life-history and ecology of the trematode genus *Renicola* Cohn, 1904. *Proc. Zool. Soc. Lond.* **126,** 1-49.

A mainly morphological study of parasites which are transmitted from clupeid fish to a number of species of sea birds.

4. FOOD AND FOOD HABITS

Betts, M. M. (1956). A list of insects taken by titmice in the Forest of Dean (Gloucestershire). *Ent. mon. Mag.* **92,** 68-71.

A list of insects found in the gizzards of tits collected monthly during 1948-51 over 350 acres of oak woodland. The list shows which of the four tits, *Parus major, P. caeruleus, P. ater* and *P. palustris,* preyed on each insect, the developmental stage of the latter, and the month in which it was found.

Butler, C. G. (1956). Some further observations on the nature of 'queen substance' and of its role in the organization of a honey-bee (*Apis mellifera*) community. *Proc. R. Ent. Soc. Lond.* (A) **31,** 12-16.

Demonstrates that queen substance is obtained by some members of a colony licking their queen and that they share it in regurgitated food with other members of their colony.

Duncan, A. (1956). Notes on the food and parasites of grey seals, *Halichoerus grypus* (Fabricius), from the Isle of Man. *Proc. Zool. Soc. Lond.* **126,** 635-644.

Food, from gut contents studies, was mainly Whiting and other gadoids, but included bottom feeding invertebrates from as deep as 37 fathoms, and algae. Seven parasites from five orders are listed, one being new for the seal.

Dunnet, G. M. (**1956**). The autumn and winter mortality of starlings *Sturnus vulgaris*, in relation to their food supply. *Ibis*, **98**, 220-230.

The food, principally leatherjackets and oats, was determined from stomach contents of birds shot regularly at roosts. Gross weight and fat deposits increased till mid-winter, and were not greatly affected by snow. The period of most acute food shortage may be early autumn, and density-governed mortality may occur at this time. (See also Dunnet, G. M., 1955, *Ibis*, **97**, 619-662. Abstract in *J. Anim. Ecol.* **25** (1956), 449.)

Gibb, J. (**1956**). Food, feeding habits and territory of the rock pipit *Anthus spinoletta*. *Ibis*, **98**, 506-530.

A study of the food and ecology of the rock pipit, mainly in Cornwall in winter. Estimates of food consumption were made. Individual territories held out of the breeding season provide their holders with food, but breeding territories are not a principal source of food.

Gillham, M. E. (**1956**). Feeding habits and seasonal movements of mute swans on two south Devon estuaries. *Bird Study*, **3**, 205-217.

A study by observation and the use of swan-proof enclosures of the influence of grazing by mute swans on salt marsh turf in the Exe and Otter valleys, and of the local seasonal movements of birds from one type of grazing to another.

Gough, H. C. (**1955**). Grazing of winter corn by the rabbit (*Oryctolagus cuniculus* (L.)). *Ann. Appl. Biol.* **43**, 720-734.

A study of the grazing patterns of rabbits on fields of winter cereals. Areas nearest to the warrens were grazed for a long period, and the crop failed; furthest areas were grazed lightly or not grazed. Severe grazing prevented the formation of secondary roots and tillers.

Jorgensen, C. B. (**1955**). Quantitative aspects of filter feeding in invertebrates. *Biol. Rev.* **30**, 391-454.

The main ecological point made is that there is a fairly constant amount of organic matter in sea water demanding a minimal efficiency ratio of water filtered to matter ingested; where the organic matter content is lower filter feeding becomes impossible.

Lewis, D. J. (**1956**). Biting times of parous and nulliparous *Simulium damnosum*. *Nature, Lond.* **178**, 98-99.

Flies caught before 1 p.m. showed more developing *Onchocerca* worms than those caught after this time. A far greater proportion of parous flies taken in morning catches may influence estimates of the infection rate. This may be linked with the apparent effect of physiological condition on the biting times of other flies.

Lockie, J. D. (**1956**). After myxomatosis. Notes on the food of some predatory animals in Scotland. *Scot. Agric.* **36**, 65-69.

Feeding preferences of the fox before and after the reduction in rabbit numbers by myxomatosis. Samples are taken from the Lowlands, Cairngorms, and Wester Ross. Changes are also reported for the buzzard, golden eagle, pine marten, weasels and stoats. The vacant ecological niche caused by myxomatosis is becoming filled by hares and voles.

Rasmussen, S. (**1956**). Nutritional preference experiments with larvae of house longhorn beetle, *Hylotrupes bajulus*. *Oikos*, **7**, 82-97.

The reactions were tested of the wood boring larvae to thin slices of pine sapwood and to filter paper both impregnated with concentrations of peptone with or without yeast extract. The results suggest a positive reaction to the nutritional value of the wood, with preference for the highest concentration of peptone.

Smith, K. G. V. (**1956**). On the Diptera associated with the stinkhorn (*Phallus impudicus* Pers.) with notes on other insects and invertebrates found on this fungus. *Proc. R. Ent. Soc. Lond.* (A) **31**, 49-55.

Thysanoptera, Lepidoptera, Coleoptera, Hymenoptera and Mollusca are also mentioned.

Thomson, J. H. (**1953**). Vole damage to trees. *Scot. For.* **7**, 111.

Damage to Sawara cypress (*Chamaecyparis pisifera*) at 10 ft from the ground at Benmore. Numerous branches, not in whorls, make access possible. Of 500 trees planted in 1930, only 40 were alive in 1934, mostly damaged. Voles show great preference for this tree and for *Robinia pseudacacia*.

Usher, G. A. (1955). Damage from mice and voles. *Quart. J. For.* **29,** 310.
In a mixed plantation, Lawson's cypress were damaged while *Thuja plicata* was untouched.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Baxter, E. V. (1956). Review of ornithological changes in Scotland in 1954. *Scot. Nat.* **68,** 1-9.
Five birds new to Scotland were recorded during the year; numerous new county records and county breeding records.

Bletchly, J. D. (1955). A little-known borer in imported softwood; *Serropalpus barbatus* Schall. (Coleoptera, Melandryidae). Review of literature and recent occurrences in Great Britain. *Forestry,* **28,** 67-72.
Biology and world distribution of a pest rare in this country, where its main importance is that the damage is indistinguishable from that caused by wood-wasps, Siricidae.

Carne, P. H. (1956). Mammals in Hampshire. *Oryx,* **3,** 200-202.
Hampshire has a rich mammalian fauna, probably owing largely to the abundance of woodland.

Boyd, J. M. (1956). The Lumbricidae of Hirta, St. Kilda. *Ann. Mag. Nat. Hist.* (12) **9,** 129-133.
The population densities of nine species are studied in various ecological zones.

Boyd, J. M., Munns, D. J. & Whitehouse, A. A. K. (1956). The birds on St. Kilda, May 1955. *Scot. Nat.* **68,** 14-22.
Notes on all species present, with a census of many.

Chambers, V. H. (1955). Further Hymenoptera records from Bedfordshire. *J. Soc. Brit. Ent.* **5,** 126-129.
Supplements the account given in 1949, *Trans. Soc. Brit. Ent.,* **9,** 197-252.

Clark, D. J. (1956). New records for *Pirata uliginosus* Thorell (Araneae, Lycosidae). *Ent. mon. Mag.* **92,** 44.
This spider, hitherto known from Merioneth, Sussex, Berkshire and Shropshire, is here recorded from Surrey, Hampshire, Cheshire and Northumberland.

Cranbrook, Earl of (1956). The mammals of Suffolk. *Oryx,* **3,** 266-270.
Discusses the mammalian fauna in general, with notes on the present rarity or abundance of various species.

Crichton, M. I., Baker, B. R. & Hanna, H. M. (1956). Records of Trichoptera from the Reading area. *Ent. mon. Mag.* **92,** 31-35.
Contains a list, with dates and localities, of 78 species collected at night, mostly in Berkshire, but also at places in Hampshire, Oxfordshire, Buckinghamshire and Surrey. 63 species occurred at one pond. A total of 93 species are now known from Berkshire.

Davis, R. A. (1956). Small mammals caught near London. *Lond. Nat.* **35** (1955), 88-89.
Mus musculus the most numerous of the seven small mammals caught in live traps in hedgerows, ricks and farm buildings from 29 September 1955 until December 1955 at two places in Surrey and until January 1956 in one in Kent. They and *Apodemus sylvaticus* about equal in abundance in hedgerows. As many as ten *Micromys minutus* trapped at one place and two in another.

de Worms, C. G. M. (1956). The moths of London and its surroundings. *Lond. Nat.* **35** (1955), 33-76.
Notes on localities, abundance, food plants and seasonal occurrence for species of Caradrinidae and Plusiidae. (Cf. 1955, *Lond. Nat.* **34** (1954), 66-107; *J. Anim. Ecol.* **25,** 201 (1956).)

Eastop, V. F. (1956). Aphids collected from Cader Idris and the Barmouth salt marsh. *Entomologist,* **89,** 101-103.
A list of some 65 species, with food plants, including several not previously known from Britain.

Godwin, G. E. (1956). A major threat to Sitka spruce? *Quart. J. For.* **50,** 119-123.
Dendroctonus (*Hylesinus*) *micans*, known in Denmark as the giant bark beetle, has spread alarmingly there since 1947, and has killed whole plantations.

Goto, H. E. (1956). *Anurophorus satchelli*, sp. n. (Collembola: Isotomidae), from Britain. *Ann. Mag. Nat. Hist.* (12) **9,** 134-139.
Much the commonest collembolan in a *Molinia* peat moss at Grange-over-Sands.

Gotto, R. V. (1956). A new asidicolous Copepod: *Lichomolgus didemni*, sp. nov. *J. Linn. Soc.* (*Zool.*) **42,** 600-602.
In the ascidian *Didemnum maculosum* in Strangford Lough.

Grensted, L. W. (1956). Diptera new to Gloucestershire. *Ent. mon. Mag.* **92,** 72.
Eight species taken in a garden.

Hallett, H. M. (1956). Hymenoptera Aculeata in Monmouthshire. *Trans. Cardiff Nat. Soc.* **83,** 1953-54, 18-21.
A list of 132 species, mainly from Raglan, Trelleck, Llanthony and Abergavenny.

Hanson, H. S. (1952). *Megastigmus* seedflies. *Quart. J. For.* **46,** 261-264.
Megastigmus is a genus of Torymidae (Hym., Chalcidoidea), many species feeding on conifer seeds. Life cycles, known infestations in Britain and present distributions are recorded.

Harper, G. W. (1956). The Macrolepidoptera of Inverness-shire—Newtonmore district. *Ent. Rec.* **68,** 91-92.
This second supplement contains thirteen additions to the main list. (Cf. 1955, *Ent. Rec.* **67,** 39-40; 1955, *J. Anim. Ecol.* **24,** 491.)

Harrison, J. W. Heslop- (1956). Lepidoptera in the Inner Hebrides. *Ent. Rec.* **68,** 97-98.
Includes seven additions to the list for Rhum. (Cf. 1955, *Ent. Rec.* **67,** 141-147, 169-177; 1956, *J. Anim. Ecol.* **25,** 202.)

Harrison, J. W. Heslop- (1956). *Rhopalomyia ptarmicae* Vallot (Dipt., Cecidomyiidae) in the Outer Hebrides. *Entomologist*, **89,** 124.
Galls of this Cecidomyiid were abundant on South Harris in 1955, which constitutes the first record from the Outer Hebrides.

Hughes, R. A. (1956). Localities for the chalk carpet (*Ortholitha bipunctaria*, Schiff.) (Lep.: Geometridae) in North Wales, 1947, 1948, 1949 and 1953. *Entomologist*, **89,** 129-130.
Records for Flintshire, Denbighshire and Caernarvonshire.

Hussey, N. W. (1952). New records of *Megastigmus* (Hymenoptera, Chalcicidae) in Scotland with a note on the first recorded parasites of *Megastigmus spermotrophus* Wachtl. *Scot. For.* **6,** 53-55.
Infestation of the seeds of conifers ; includes three species new to Britain.

Hyatt, K. H. (1956). British mites of the genus *Pachyseius* Berlese, 1910 (Gamasina-Neoparasitidae). *Ann. Mag. Nat. Hist.* (12) **9,** 1-6.
Two British species in leaf litter and in lake high-water debris.

Jackson, D. J. (1956). The capacity for flight of certain water beetles and its bearing on their origin in the Western Scottish Isles. *Proc. Linn. Soc. Lond.* **167,** 76-96.
Less than half of all specimens can fly, several species being entirely flightless. These species must have reached the islands via a land connection.

Johnson, A. L. (1956). Seal migration. *Nature in Wales*, **2**, 267-270.
Based on recent work in west Wales on the recovery of ringed grey seals.

Massee, A. M. (1955). Notes on some interesting insects observed in 1954. *Rep. East Malling Res. Stn.* (A) **38,** 133-136.
Short notes on some of the interesting insects and mites observed on fruit trees in 1954.

Maxwell, H. A. (1953). Grey squirrels in Scotland. *Scot. For.* **7,** 92-94.
At present mainly occurring in 8 counties in central Scotland. General notes and methods of destruction.

Morgan, N. C. (1956). The occurrence of *Dixa filicornis* Edwards (Dipt. Culicidae) in central Perthshire. *Entomologist*, **89**, 71-72.

Adults of this species, hitherto known only from the type locality of Sussex, were taken in emergence traps over Loch Dunmore during April-May and August-October, 1954-55. Most taken over water 6-12 in. deep with a bottom of leaves on mud, but one taken over water 6 ft deep with a bottom of bare mud.

Niblett, M. (1956). The flies of the London area. III. Trypetidae. *Lond. Nat.* **35** (1955), 82-88.

Localities, seasonal life-history and food plants for the 49 Trypetids known to occur within a 20-mile radius of St. Paul's Cathedral.

Perkins, E. J. (1956). *Microarthridion fallax*, a species of Harpacticid Copepod new to science from Whitstable, Kent. *Ann. Mag. Nat. Hist.* (12) **9**, 108-111.

In sand and mud. A key to the genus is given.

Rae, B. B. & Wilson, E. (1956). Rare and exotic fishes recorded in Scotland during 1954. *Scot. Nat.* **68**, 23-38.

Notes on 38 species; the most notable feature of the year was the phenomenal number of records of the deal-fish, *Trachypterus arcticus*.

Reynoldson, T. B. (1956). The occurrence in Britain of the American Triclad *Dugesia tigrina* (Girard) and the status of *D. gonocephala* (Duges). *Ann. Mag. Nat. Hist.* (12) **9**, 102-105.

Records of *gonocephala* probably refer to *tigrina*, which has been introduced several times.

Reynoldson, T. B. (1956). Observations on the earthworms of North Wales. *Northw. Nat.* (N.S.) **3** (1955), 291-304.

Nineteen species were recorded. Information on the ecological distribution is given. The species composition in cultivated soils broadly resembles that in lowland Scotland.

Reynoldson, T. B., O'Connor, F. B. & Kelly, W. A. (1956). Observations on the earthworms of Bardsey. *Rep. Bardsey Bird Field Obs.* **1955**, 31-39.

Nine species occur on the island, which is off the coast of Caernarvonshire. Samples were taken from various habitats and estimates made of numbers and biomass.

Robinson, D. M. (1956). Craneflies (Dipt., Tipulidae) from Northumberland. *Ent. Mon. Mag.* **92**, 72.

Five additions to the county list.

Sage, B. L. (1956). Notes on some Coleoptera from South Hertfordshire. *Ent. Rec.* **68**, 112-113.

Lists of twelve species from Aldenham Reservoir and thirty from Cuffley Greatwood, both scheduled as Nature Conservation Areas.

Salmon, H. M. (1956). Ornithological Notes 1953-54. *Trans. Cardiff Nat. Soc.* **83** (1953-54), 22-24.

A list of 41 species, including two new to Glamorgan, the Squacco Heron and the Bridled Tern.

Scudder, G. G. E. (1956). A contribution to a survey of the distribution of the Hemiptera-Heteroptera of Wales. *Ent. Mon. Mag.* **92**, 54-64.

This extensive list includes several species new to Wales.

Spencer, K. A. (1956). The British Agromyzidae (Dipt.). *Proc. S. Lond. Ent. Nat. Hist. Soc.* 1954-55, 98-108.

A large number of additions to the British list, four deletions, and an interim check list of British representatives, comprising some 250 species.

Taylor, W. L. (1954). Squirrels in Great Britain. *Forestry*, **27**, 63-68.

The distribution in 1953 and the habits of *Sciurus vulgaris leucourus* and *S. carolinensis* are discussed and their control considered.

Went, A. E. J. & Vickers, K. U. (1956). Salmon movements around Ireland—VI. From Portballintrae, Co. Antrim (1953 and 1954). *Proc. R. Irish Acad.* (B) **58**, 17-21.

More movements to the west than otherwise, most movements at less than five miles per day.

White, E. (1956). The hydroid *Hydranthea margarica* (Hincks) in Scottish waters. *Scot. Nat.* **68**, 39-42.

The most northerly and first Scottish record on *Flustra* at Sanda island, Argyll.

Williamson, K. (1956). Birds and Lepidoptera in Anticyclonic airstreams. *Ent. Rec.* **68**, 95-97.

Large invasions of Fair Isle by migrant birds as a result of down-wind drift in anticyclonic airstreams from Europe are often accompanied by influxes of migrating *Plusia gamma*. Evidence of a link between the migration of lepidopterous species and anticyclonic airstreams, similar to that between the latter and birds, was provided by captures in a mercury-vapour trap in late August 1955 and supported by similar captures on the Island of Canna (Hebrides) and visual observations at Great Saltee (off south-eastern Ireland).

Woodroffe, G. E. (1956). Miscellaneous records of Hemiptera-Heteroptera captured during 1955. *Ent. Mon. Mag.* **92**, 47-48.

Includes information on the habitat and food plants of several uncommon species.

6. STUDIES ON BEHAVIOUR

Andrew, R. J. (1956). Territorial behaviour of the yellowhammer *Emberiza citrinella* and corn bunting *E. calandra*. *Ibis*, **98**, 502-505.

Yellowhammer territories were based on a hedge, those of corn buntings were centred over cornfields. In both the formation and maintenance of the bond between the sexes appeared to be the prime function.

Armstrong, E. A. (1956). Territory in the wren *Troglodytes troglodytes*. *Ibis*, **98**, 430-437.

The males are strongly territorial and polygamous. Territory leads to dispersal and is of use in pair formation. It provides a foraging area in which roosting and nesting sites are known. Basically territorialism is concerned with reproduction.

Ash, J. (1956). Mimetic posturing of red-backed shrikes. *Brit. Birds*, **49**, 178-180.

In the New Forest red-backed shrikes were so inconspicuous that they were rarely seen unless specially searched for. On three occasions in 1955 cocks were found in a mimetic posture which may be significant in relation to the apparent scarcity of the species, and may have high survival value.

Blank, T. H. & Ash, J. S. (1956). The concept of territory in the partridge *Perdix p. perdix*. *Ibis*, **98**, 379-389.

Territory is of two types, covey territory (late summer to early winter) and pair territory (late winter to early summer). Unmated cocks show no territorial behaviour. Territory distribution is closely associated with food supply.

Church, H. F. (1956). The roosting times of the swift. *Bird Study*, **3**, 217-220.

During 1954 and 1955 the time of going to roost of swifts at Berwick on Tweed was closely correlated with time of sunset. Flying and feeding times are regarded as functions of day-length, this determining later arrival and early departure near the northern limit of the range.

Conder, P. J. (1956). The territory of the wheatear *Oenanthe oenanthe*. *Ibis*, **98**, 453-459.

Wheatears pair for life and usually occupy the same territories each year. Migrants hold small territories while resting when on passage. Though territories supply sufficient food, their first importance is as breeding areas, places most suitable for breeding being occupied before the best foraging areas.

Ellis, P. E. (1956). Differences in social aggregation in two species of locust. *Nature, Lond.* **178,** 1007.

Locusta migratoria and *Schistocerca gregaria* show differences in the time of onset of gregarity. *Locusta* appears more readily dispersed in the laboratory, and probably the patchy physical environment is more important in the retention and the formation of groups than in *Schistocerca*.

Gibb, J. (1956). Territory in the genus *Parus*. *Ibis*, **98,** 420-429.

All species studied are territorial in the breeding season, but in winter territorial behaviour is variable, correlated with food supply.

Goodwin, D. (1956). Further observations on the behaviour of the jay *Garrulus glandarius*. *Ibis*, **98,** 186-219.

Aspects of the behaviour of wild and captive birds not dealt with in a previous paper. (See also Goodwin, D., 1951, *Ibis*, **93,** 414-442 and 602-625. Abstract in 1955, *J. Anim. Ecol.* **24,** 247.)

Goodwin, D. (1956). The problem of birds escaping from captivity. *Brit. Birds*, **49,** 339-349.

Notes on the families usually kept in captivity, the behaviour of escaped birds, and points regarding their condition and plumage which help their recognition.

Hale, W. G. (1956). The lack of territory in the redshank *Tringa totanus*. *Ibis*, **98,** 398-400.

Observations on a Lancashire population. No area was defended against other redshanks, but after hatching a definite area round the nest was defended against predators.

Hinde, R. A. (1956). The biological significance of the territories of birds. *Ibis*, **98,** 340-369.

An introduction to and partial summary of a series of contributions on territory in individual species. It is concluded that territorial behaviour has diverse functions, but in most species is not primarily concerned with food.

Lockie, J. D. (1956). Winter fighting in feeding flocks of rooks, jackdaws and carrion crows. *Bird Study*, **3,** 180-190.

Describes aggressive behaviour in relation to mating and food, and argues that the social hierarchy established by food fighting implies that birds are liable to meet food shortage, the behaviour then ensuring unequal distribution of what food there is, some birds obtaining enough, others starving.

McCartan, L. & Simmons, K. E. L. (1956). Territory in the great crested grebe *Podiceps cristatus* re-examined. *Ibis*, **98,** 370-378.

Possible functions are discussed but no definite conclusions are drawn.

Marler, P. (1956). Territory and individual distance in the chaffinch *Fringilla coelebs*. *Ibis*, **98,** 496-501.

Territories are held mainly in the breeding season, the smallest, in marginal habitats, being the most fiercely defended. They provide little food.

Marler, P. (1956). The voice of the chaffinch and its function as a language. *Ibis*, **98,** 231-261.

Recordings made with a tape recorder and analysed on a sonograph. Fourteen basic calls recognized, and the communicatory function of voice assessed by studying the responses of other chaffinches. Inter-specific communication occurs through alarm calls which are difficult for predators to locate. (See also Marler, P., 1952, *Ibis*, 94, 458-472. Abstract in 1955, *J. Anim. Ecol.* **24,** 496.)

Matthews, G. V. T. (1955). An investigation of the 'chronometer' factor in bird navigation. *J. Exp. Biol.* **32,** 39-58.

Exposure to irregular light and darkness, followed by a false daily rhythm in advance or retard of the natural one, resulted in wrong orientation to directions which were predictable by the sun navigation hypothesis.

Mountfort, G. (**1956**). The territorial behaviour of the hawfinch *Coccothraustes coccothraustes*. *Ibis*, **98**, 490-495.

Hawfinches nest solitary or in colonies. Solitary pairs defend a territory throughout the nesting period. In colonies males defend their nest tree from other males till the eggs are laid, but thereafter only communal defence against predators occurs. Success is one-third less in solitary nests.

Page, F. J. Taylor (**1956**). Roe deer and ergot. *Oryx*, **3**, 270-271.

Criticizes the idea that roe are attracted to their ringed areas by ergotized grasses. Considers that all ring-making activity has probably some erotic background.

Pratt, J. G. (**1955**). An investigation of homing ability in pigeons without previous homing experience. *J. Exp. Biol.* **32**, 70-83.

Pratt, J. G. & Thouless, R. H. (**1955**). Homing orientation in pigeons in relation to opportunity to observe the sun before release. *J. Exp. Biol.* **32**, 140-157.

In general this provides support for the sun navigation hypothesis.

Simmons, K. E. L. (**1956**). Territory in the little ringed plover *Charadrius dubius*. *Ibis*, **98**, 390-397.

The little ringed plover, the ringed plover *Ch. hiaticula*, and the Kentish plover *Ch. alexandrinus* regularly defend territories against each other. The only obvious function is that the spacing-out of pairs reduces the danger of predation of nests.

Snow, D. W. (**1956**). Territory in the blackbird *Turdus merula*. *Ibis*, **98**, 438-447.

Studied at Oxford in a garden habitat holding 11 to 17 pairs. Old males maintain their territories all the year round, usually with their mates. Territories are not used principally as a source of food : their main function appears to be for breeding.

Stokes, B. M. (**1956**). A chemotactic response in wheat bulb fly larvae. *Nature, Lond.* **178**, 801.

Experiments suggest that location is by means of response to chemical diffusion.

Thompson, J. L. Cloudsley- (**1956**). Notes on Arachnida, 25.—An unusual case of phoresy by false-scorpions. *Ent. Mon. Mag.* **92**, 71.

Allochernes dubius, which usually occurs under stones and vegetation, on *Oligolophus meadii*. Other records of phoresy by false scorpions on harvest spiders are reviewed.

Tinbergen, N. (**1956**). On the functions of territory in gulls. *Ibis*, **98**, 401-411.

Territory in gulls is important in assisting and preventing interference with pair formation, and in reserving, except in the kittiwake *Rissa tridactyla*, space round the nest site to provide known shelter for the young. In the kittiwake territory is confined to the nest ledge.

Wallace, D. I. M. (**1956**). Song-flight of green sandpiper on passage. *Brit. Birds*, **49**, 323.

The song-flight, observed in early October, was sustained for fifteen minutes.

Wallace, D. I. M. (**1956**). Recognition and repulsion of a predator by spotted flycatchers. *Brit. Birds*, **49**, 328.

A pair of spotted flycatchers displayed at and mobbed grey squirrels (*Sciurus carolinensis*) when they visited their territory, and a squirrel was chased across a lawn by them.

7. REPORTS OF ORGANIZATIONS

Bardsey Bird and Field Observatory (**1956**). Report, 1955. pp. 52.

Contains reports on bird ringing and birds seen on the island, and papers on the fauna of marine rocks and the earth-worms of the island, which is off the coast of Caernarvonshire.

Cambridge Bird Club (**1956**). Twenty-ninth Annual Report, 1955. pp. 28.

Faunistic notes; counts of waders and wildfowl; notes on migration in the Wash.

Cornwall Bird Watching and Preservation Society [**1956**]. Twenty-fifth Annual Report, 1955. pp. 70.

Faunistic notes, arrival and departure of migrants and a paper on the effect of myxomatosis on the buzzard in Cornwall.

Derbyshire Ornithological Society (1956). Report for 1955. pp. 23.

The first annual report of this new society consists almost entirely of faunistic notes and dates of the arrival and departure of migrants.

des Forges, G. & Harber, D. D. (1956). The Sussex Bird Report, 1955. pp. 20.

Consists almost entirely of classified faunistic notes.

Devon Bird-watching and Preservation Society (1956). Twenty-eighth Report, 1955. pp. 80.

Mainly faunistic notes, but includes reports on black redstart and spotted flycatcher inquiries, monthly wildfowl counts, and the sanctuary at Chapel Wood, Spreacombe.

Eggeling, W. J. (1956). Isle of May Bird Observatory and Field Station. Report for 1953-55. *Scot. Nat.* **68,** 43-56.

Notes on bird migration and ringing, changes in status of various birds, and myxomatosis on the island (Firth of Forth).

Fair Isle Bird Observatory Trust (1956). Bulletin, **3,** nos. 1, pp. 1-48 & 2, pp. 49-108.

Numerous papers on bird migration on Fair Isle, as well as in other parts of the British Isles, including Foula, South Shetland, the Butt of Lewis, Coll (Inner Hebrides), Great Saltee (Co. Wexford) and Portland Bill; also short papers or reports on breeding studies of the great and arctic skuas on Fair Isle, bird ectoparasites on Fair Isle and Skokholm, and the migration of Lepidoptera on Skokholm.

Lundy Field Society (1956). Ninth Annual Report, 1955. pp. 43.

In addition to the usual list of birds seen on the island, which is in the Bristol Channel, there are shorter reports on bird ringing, bird ectoparasites, work on nesting sea birds, visible bird migration, and work on wild and feral mammals, including a series of censuses of grey seals.

Middle-Thames Natural History Society (1956). Middle-Thames Naturalist, no. **8,** pp. 32.

Faunistic notes on birds and a check-list of the mammals of parts of Buckinghamshire and Berkshire.

Norfolk Naturalists Trust (1956). The Norfolk Bird Report, **1955.** pp. 62.

Besides classified faunistic notes, includes reports on the breeding birds of the Trust's sanctuaries, a huge starling roost estimated to hold 3½ million birds, and the Cley Bird Observatory.

Oundle School Natural History Society (1956). Annual Report, **1955.** pp. 62.

Contains reports on bat ringing, a census at a pipistrelle roost, birds, wildfowl counts, bird ringing, fish, Lepidoptera, beetles, freshwater gastropods, Rotifera, the life cycle of *Proales wernecki* (Rotifera); the comparative biology of *Asellus*, *Eucrangonyx* and *Gammarus* (Crustacea); and the animals of opencast spoil-heaps.

Royal Society for the Protection of Birds (1956). Sixty-fifth Annual Report: Bird-Protection, 1955. pp. 44.

Includes notes on birds seen at the Society's sanctuaries in Suffolk (Minsmere, Havergate, North Warren, Breckland), Kent (Dungeness), Devon, Cheshire, Pembrokeshire (Grassholm), Orkney and Shetland.

BRITISH ECOLOGICAL SOCIETY

SPRING MEETING, LONDON

27-28 MARCH 1956

The Spring Meeting was held in the rooms of the Nature Conservancy, 19 Belgrave Square, by kind invitation of the Director-General of the Conservancy. The meeting was devoted to a Symposium on 'Production'.

27 *March*. The meeting opened at 2 p.m. when Mr E. M. Nicholson, Director-General of the Nature Conservancy, welcomed the Society. The President informed the Society of the absence through illness of Professor Pearsall who was to have introduced the symposium, and expressed the regret of all present. In his absence, the subject of the symposium was introduced by Mr E. D. Le Cren, who described the aim of the meeting as an attempt to clarify ideas which have emerged from recent work on quantitative aspects of growth and production in animal and plant populations. Three concepts were discussed in some detail in the hope that uniformity of terminology might be achieved by subsequent contributors. These were: *Stock*—the total weight (or 'biomass') of a population of a species at any one time. *Production*—the total amount of living matter produced by a group of organisms over a period of time, irrespective of whether it survives throughout that time. This represents the growth of individuals. *Crop*—that part of the production which passes on to the next direct link in a food chain, or is consumed by Man.

The first paper was given by Dr J. D. Ovington on 'Forest Production'. Dr Ovington commented that in order to make the best use of land the productivity of the whole plant of cultivated species must be considered, and that little was hitherto known of dry-matter production in the various parts of a tree — canopy, bole and root. He presented data for an age-series of *Pinus sylvestris* woodlands to illustrate techniques for estimating production in single trees and forest stands. Changes in form were noted in the individual tree as the plantation in which it stands matures, and it was shown that with increasing age the living canopy decreases in importance (with regard to the proportion of total dry matter contained), while the bole and to a lesser extent the rootstock increase in this respect. In considering production in stands of trees, Dr Ovington demonstrated changes with increasing age which were markedly different in the different parts of the trees. Current annual increments for the stand as a whole show a conspicuous increase after thinning operations at 20 years, but a figure of 13×10^3 Kg/hectare/annum was quoted as a mean for the dry matter increment. The productivities of the components of the entire woodland ecosystem, as distinct from that of the trees, were briefly compared, and it was shown that figures for ignition loss and carbon were higher in tree boles and canopies than in the ground flora and humus or mineral soil, but that nitrogen was greater in amount in the soil, and quantities in the ground flora and humus were at least as large as in the trees. Potassium was also present in the flora and humus in quantities equivalent to those in the trees.

Mr J. A. Gibb followed with a paper on 'Production in some forest birds and their prey', reporting work done under the auspices of the Breckland Research Unit of the Edward Grey Institute. An investigation of the relationship between the stock and production of tits (Paridae) and the stock of insects in plantations of *Pinus sylvestris* and *Pinus nigra*, as compared with that in broadleaved woods, showed that the population of tits in the pine plantations was normally one-fifth of that in mixed broad-leaved woods. There are marked annual fluctuations, the stock being greatest in mid-summer, immediately after the breeding season, declining abruptly in July and August and more slowly through the winter. The reproductive rate of tits is slightly higher in pine plantations than in broad-leaved woods. This is related to the longer season of caterpillar production in the pines where a peak is reached in July and is followed by a second flush in August, whereas in oaks the peak occurs at the time of formation of new leaves in

May and is followed by a rapid fall. It is estimated that tits eat less than 10% of the caterpillar stock in summer. Comparable measurements are more difficult to obtain in winter, but tentative results suggest that the tits may eat a rather higher proportion of the stock of their insect food. For instance, in three successive winters the tits are known to have eaten between 25% and 50% of the stock of larvae of the eucosmid *Laspeyresia conicolana* which passes the winter in the pine cones. Pine-seed is an important food of tits, notably in spring and late summer. The tits store many seeds in autumn and eat them later in the winter. The production of pine cones was measured in 1955; red squirrels ate about 25% of the stock.

In a lively discussion which followed these papers, members taking part were Professor G. C. Varley, Professor N. A. Burges, Dr A. S. Watt, Professor J. B. Cragg, Mr E. M. Nicholson, Dr D. Lack, Dr E. W. Jones, Dr A. S. Thomas, Mr E. D. Le Cren, Mr O. J. W. Gilbert, Mr J. Chear, Mr J. L. Harper, Dr A. J. Rutter and Dr C. H. Gimingham. The view was expressed that stands of single tree species give rise to such artificial ecological conditions that production in plant and animal populations may not be in balance. Alterations in rates of production with the progress of successional change in vegetation and soil and the possibility of a secondary fall in production as podsolization takes place were also considered. Dr Rutter gave some interesting information on changes in the 'unit leaf rate' of scots pine with increasing age, and commented that although the assimilation rate is low, the trees are actively assimilating throughout the year, the rate in winter being about one-quarter of that in summer.

After tea at 4 p.m., the symposium was resumed with a paper by Dr F. H. Whitehead on 'Productivy in Alpine Vegetation'. Dr Whitehead described a series of plant communities on limestone detritus on Monte Maiella in the Central Apennines, and considered effects upon them of exposure to wind. Plant height, inflorescence height, number of species and variety of growth forms were related to this factor, as were % cover, annual yield, and quantities of inorganic nutrients in the cropped material. Verification of the relationship between height and exposure was obtained by the construction of low walls round permanent quadrats. Dr Whitehead claimed that plants grown in high wind velocities show slower growth rates than those in calm conditions, and suggested three types of reaction: (1) species which by their growth behaviour may be regarded as exposure evaders, e.g. *Cerastium atrovirens*; here the dry weight curve shows little falling off with increase in wind velocity. (2) Species which, although showing a diminution of height with increase in wind velocity, exhibit comparatively small decreases in dry weight, e.g. barley. (3) Species in which both height and dry weight rapidly decrease with increase in wind velocity, e.g. *Senecio nebrodensis*. Productivity in alpine communities, as measured by a variety of criteria, may thus be related to the degree of shelter afforded by the irregularity of the surface, but the reactions of individual species disclose a variety of physiological behaviour which requires independent autecological investigation.

The following contribution was entitled 'The Plant cover: the stock of vegetation types'. In the absence of Professor W. H. Pearsall, data obtained by him and Dr E. Gorham were presented by Dr P. J. Newbould. Estimates have been made of the stock of several British vegetation types by cutting, drying and weighing the above-ground parts at the end of the growing season. Sample sites, where possible, contained only one species showing full dominance and representing the entire vegetation production of that habitat. Samples were mainly taken in groups of five 625 sq.cm quadrats arranged as the holes in a ladder. Results from about 20 vegetation types studied fall between 4000 and 12 000 kg/ha, and this is thought to be approximately equivalent to the annual production of these vegetation types. It resembles closely results obtained for woodland production by Ovington. Base-rich habitats tend to show a higher production than base-poor habitats, but there seems little difference between wet and dry habitats. This upper limit of 12 000 kg/ha may be determined by the annual amount of photosynthesis, a function of light, climate, and the effects of temperature and soil conditions on leaf growth.

In a paper on 'Energy Relations in the Soil Fauna', Mr A. Macfadyen argued that it is only possible to balance the production equation within a community by taking as a

common measure the energy (in calories) which is on the one hand derived by plants from sunlight, and on the other dissipated by successive 'consumer layers' of the heterotrophic organisms. The extraction and census of species of Collembola, mites, millipedes, woodlice, beetles and spiders from an area of *Brachypodium* grassland were described and details given of laboratory apparatus designed to measure respiration rates under conditions simulating those in the field as closely as possible. Key factors such as temperature were also measured in the field. Energy consumption can be used as a yardstick to indicate the exploitation of food materials by soil animals, irrespective of their place in the food chain. Of this intake, about one-third may be liberated in respiration, the rest remaining in excreta, etc., dead bodies and in predators and decomposition organisms. With the evolution of 'higher' groups, respiration rates and therefore specific activity increases markedly.

Dr E. W. Jones, Professor G. C. Varley, Mr E. D. Le Cren, Professor J. B. Cragg, Mr J. G. Skellam, Mr A. Ibbotson, Dr K. H. Mann and Mr Heath took part in the discussion which followed these papers.

28 *March*. The symposium was resumed at 10.30 a.m. when Mr J. Corlett spoke on 'Marine Plankton Production'. Describing work carried out mainly in the Barents Sea, Mr Corlett outlined the food chains, and presented data obtained by a variety of methods for the measurement of stock and production in the first two stages of the chain, the phytoplankton and zooplankton. Different estimates of production were compared, the figures in general coming within the range for land vegetation quoted in various papers on the previous day.

Dr J. H. Mundie, discussing 'The Production of Chironomids in Lakes', clearly demonstrated differences in the stock of non-biting midges in silted and unsilted lakes, showing that the bottom fauna was directly correlated with the plankton, and inversely with oxygen tension, and in oligotrophic lakes with dissolved organic content. As erosion of the watershed contributes materials to lakes, the fauna increases, food being the main factor controlling the animal numbers. In a detailed example of a profundal community of seven species, estimates were given of the annual crop of all species based on their emergences, and it was shown that the carnivores have the highest total emergences per number of benthic larvae. The total crop of all species is not less than 60% of the late winter stock. Mr Mundie concluded by sketching two 'trophic series' in lakes: (1) nutrients→plants→herbivores→carnivores; (2) faeces and detritus→detritus feeders→ carnivores; these being linked not linearly but 'turbulently'.

In a paper on 'Some Estimates of Fish Production and its Exploitation' Mr E. D. Le Cren described fish as peculiar animals in their extreme plasticity in adult size and growth-rate. A study of their population numbers alone is therefore of little use; growth has also to be taken into account; together, number × growth = production. Early classical work by Petersen and his colleagues in Denmark estimated stocks of *Zostera*, bottom fauna, and fish, etc. Some of their findings are now discounted, but in principle they were on right lines. Foerster & Ricker estimated production of salmon fry in Cultus Lake and the eventual crop of migrants to the sea. Interesting relationships between population density, production and predation were revealed. Allen estimated production of trout in the Horokiwi River, New Zealand, and showed how much production took place early in life and how little was cropped. It is also possible to calculate first approximation estimates for the production of perch and pike in Windermere. These estimates are complicated by an experimental fishery but show the possibilities of estimating the production of a prey and its principal predator. Fisheries, or any similar form of exploitation, are only possible because natural populations will respond to exploitation by increases in the rate of production. In fish this takes place in three ways: (1) by a density-dependent effect on natural mortality; (2) by a density effect on growth-rate; and (3) by the relation between growth-rate and average fecundity.

A discussion followed, centring on the factors influencing production and the effects of cropping upon production, those taking part being Professor G. C. Varley, Mr J. G. Skellam, Professor J. B. Cragg, Dr K. H. Mann, Mr A. Macfadyen, Dr E. W. Jones, Dr B. B. Parrish and Dr A. S. Watt.

At 2 p.m. Mr C. W. R. Spedding contributed a paper on 'The Agricultural Produc-

tivity of Grassland'. He pointed out that grassland research is concerned with potential production and the capacity of an area to yield products of agricultural value. A problem arises in the measurement of production, since the figure obtained varies according to the method used, e.g. whether by cutting the pasture or by recording the live-weight increase of animals grazing it. Similarly different systems of cutting or grazing treatment give different estimates. Thus grassland production can be stated only within the context of a given system of management. A distinction must also be drawn between production in terms of grass and its value to the animal, largely due to the seasonal growth curve of herbage. The agriculturist has to achieve a balance between herbage production and the nutritional requirements of a population of grazing animals. A complication is introduced by the presence of internal parasites which may be responsible for a loss of 15% in the animal production and influence the accuracy of any measurement of grassland production using sheep.

Dr R. E. Hughes next gave a paper on 'The Productivity of Snowdonian Sheep Walks'. Quoting work by Phillips *et al.* showing that climatic factors have a marked influence on livestock productivity in Wales, Dr Hughes demonstrated the existence of steep rainfall gradients in the Snowdonia area in which the productivity of sheep walks had been investigated, using stock number per acre as a good guide to production. There was also a difference in the soils, which in some parts of the area are derived from basic ashes, dolerites and acidic riolites, and in others from slates and sedimentary rocks. Glacial drifts, however, are charged with materials from both types of source, and the sheep walks are mainly on the areas of igneous rock. The soils are increasingly podsolized in the regions of higher rainfall, approaching gleyed podsolic conditions. Dr Hughes concluded that the major variance in productivity in terms of sheep is due to ecological factors of which rainfall is the principal one. Below a critical rainfall level, soil and vegetation also have a considerable influence.

The final paper by Mr A. D. Bradshaw was entitled 'The Genecology of Productivity of Grasses'. Here, production was considered from an evolutionary point of view. There is a considerable amount of general evidence that plants can be too vigorous or too slow-growing for a particular environment. There is in fact an optimum productivity for a particular environment, the amount depending on various factors such as soil fertility, competition, exposure, etc. Thus plant species in being adapted to particular environments have particular productivities; productivity is as much a characteristic of a species as height or size of flowers. For example arctic-alpines are usually species of low productivity, while plants of rich grassland are of high productivity. If a species occupies several different habitats and if it is differentiated by natural selection into a series of different ecological races, these races should differ in productivity just as much as in any other character. Stapledon (1928) pointed out that in cocksfoot the highest yielding plants were to be obtained from rough places and hedgerows. A comparison of the productivity of populations of *Agrostis tenuis* from a number of different habitats when grown in an experimental garden showed significant and considerable differences in the mean productivity of each population. Plants from grazed habitats in all cases had lower productivities than those from ungrazed areas, and ones from less fertile habitats had lower productivities than those from the more fertile. The lower-yielding plants were those from the very extreme environment of a lead-mine dump, the highest from a piece of rough fertile grassland in Pembrokeshire. In plants originally growing as weeds of arable land the greater part of the production was directed to the formation of panicles; while in plants from heavily grazed places the greater part was directed to the formation of vegetative growth. Thus it seems that productivity, in common with ordinary morphological characters, is an attribute of plant species and is one upon which natural selection can act.

Professor G. C. Varley, Dr E. W. Jones, Dr A. S. Thomas, Mr J. G. Skellam, Mr O. J. W. Gilbert, Dr P. J. Newbould, Mr E. D. Le Cren, Dr A. S. Watt and Major C. W. Hume participated in the concluding discussion. Dr Watt pointed out that even where a species is dominant it may not always be at its ecological optimum, and he was therefore disinclined to accept the suggestion that production remains approximately constant in dominant stands even under differing habitat conditions.

During the meeting Mr V. S. Summerhayes, Hon. Treasurer, presented the audited accounts for the previous year 1955 and reported briefly upon them.

The President read a letter from the Indian Council of Ecological Research, intimating the preparation of bulletins on applied ecological subjects containing papers from specialists in different countries. Contributions from British ecologists were sought, and members interested in this project are asked to get in touch with the Secretary of the Indian Council of Ecological Research, Office of the Technical Secretariat, P.O. New Forest, Dehra Dun, India.

The thanks of the meeting for the hospitality extended by the Director-General and Staff of the Nature Conservancy were expressed by the President.

C. H. GIMINGHAM

SUMMER MEETING IN THE LAKE DISTRICT

12-17 JULY 1956

For this meeting the Freshwater Biological Association and the Merlewood Research Station of the Nature Conservancy acted as joint hosts. The F.B.A. Laboratory at The Ferry House, on the west shore of Lake Windermere, formed the headquarters and provided comfortable accommodation for some of the eighty members and guests who attended the meeting. At the soirée on 12 July it was immediately apparent that most careful staff-work had been done to ensure the smooth running of a large variety of activities. Timetables, notes and sketch-maps were provided for the ensuing five days, and other explanatory material was on exhibit.

On the morning of Friday 13 July Mr H. C. Gilson opened the proceedings with a warm invitation to members to inspect the work in progress at the F.B.A. Laboratory. After Mr Le Cren had explained various practical matters, members had a choice of four places to visit during the day, all within a few miles of Ferry House: the North Fen of Esthwaite Water; the more or less aquatic communities in Pull Wyke, a bay at the north end of Windermere; the Wraymires fish-hatchery overlooking Esthwaite Water; and the tarns on Claife Heights, between Esthwaite and Windermere, where experiments are in progress on the populations of aquatic invertebrates and fish.

The Esthwaite Fen attracted the largest attendance, and many members enjoyed the stimulating guidance of Professor W. H. Pearsall over ground (now a National Nature Reserve) which he has had under observation for more than 40 years. The many findings reported by him in the *Journal of Ecology*, and recounted by Tansley in *The British Islands and their Vegetation*, cannot be summarized here. The most striking contrast to be seen in a short visit is between the carr of *Salix atrocinerea*, on highly organic silt rich in minerals and with pH above 5, and the developing bog (*Molinia*, *Myrica*, *Narthecium*, *Sphagnum*, etc.) at the east side where the water-supply, unlike that of the fen and carr, consists only of rain. Anomalous-looking stands of *Salix*, with some alder, in the bog region mark the emergence of telluric water in springs. Professor Pearsall emphasized one important and surely often neglected ecological factor, demonstrable here because of the long continuity of observation, namely the influence of 'accidents' in determining local variants of vegetation which may last indefinitely. In this case the accident was the lodging of a floating log, against which *Phragmites* litter accumulated to such an extent that the normal succession was locally altered, with effects still easily visible, although the initial cause would never now be detected.

On Saturday 14 July Professor Pearsall was again in charge, the objective being the Old Man of Coniston (803 m = 2635 ft) and the neighbouring fells. The arrangements included a thorough demonstration of rain as a factor in mountain habitats. The transport, a variety of vehicles belonging to the F.B.A. and to B.E.S. members, stopped at Coniston station or farther on up the Walna Scar Road. A walk of another mile west-

wards along this track skirted the foot of Little Arrow Moor, below which Professor Pearsall pointed out an extensive prehistoric settlement site at about 270 m (900 ft) altitude, occupying the gently sloping shelf between the glacially steepened valley-slopes below and the steep mountain slopes above. On the latter bracken extends upwards for 150 m (500 ft) or more altitudinally and marks the area probably occupied by oak-wood before the destruction of high-level forest perhaps two or three thousand years ago. Professor Pearsall reminded us that the Lake District mountains have long been severely over-grazed, so that the gentler slopes have been depleted of mineral nutrients and now bear Nardetum of negligible pastoral (or other) value, while the soils on steeper slopes, although more readily replenished with minerals, meet the other danger of erosion.

The westerly route soon reached a point where a party led by Dr Macan diverged northwards to Goat's Water to examine the tarn fauna. The other members held to the Walna Scar Road as far as the Coniston-Duddon watershed and then also struck northwards, ascending obliquely up a *Nardus*-covered slope interrupted by scree-lines in which *Rhacomitrium lanuginosum* was prominent. The rocky summit of Dow Crag afforded some shelter from the north-easterly gale and lunch was eaten rapidly. A circuit turning towards the east, then south-east, led back to the transport. It included the summit of the Old Man, but the recurring rain was so severe that the good pace set by Professor Pearsall was generally appreciated. In wet flushes passed on the ascent a few characteristic plant species were noticed, e.g. *Philonotis fontana*, *Cochlearia alpina* and *Saxifraga stellaris*. *S. aizoides* was seen by Dr Melville, who also found *Sedum roseum* on the crags. *Epilobium pedunculare* occurred plentifully in small watercourses. Floristic observations otherwise were somewhat damped by the conditions, although the bright green of *Cryptogamme crispa* was frequently noticeable. A tea of memorable excellence at Coniston preceded the homeward drive.

The weather on Sunday 15 July was more reasonable, although misty. Coaches and cars assembled at about 11 a.m. at Sunbiggin Tarn, lying in an area of heather moorland, Tarn Moor, roughly midway between Tebay and Kirkby Stephen. Dr M. W. Holdgate explained the topographical and ecological features of this rich area, where Carboniferous Limestone is partly overlain by drift. Details are given in his papers in *J. Ecol.* 1954 and 1955. The tarn, conspicuously tenanted by black-headed gulls, is almost surrounded by fen which varies greatly in wetness and in floristic composition. Of about ten Carices present, *C. rostrata* is the most widespread. *Cladium mariscus* is here at its highest British station. *Eleocharis uniglumis* occurs with *E. palustris*. A very incomplete impression of the vegetation observed on this visit may be given by mentioning some of the dicotyledons in flower: *Filipendula ulmaria*, locally dominant on higher levels, *Cardamine amara*, *C. pratensis*, *Myosotis caespitosa*, *M. secunda*, *Pedicularis palustris*, *Ranunculus lingua*, *Senecio aquaticus*, *Stellaria alsine*, *Veronica scutellata*. It is no easier to do justice briefly to the rich, partly calcicole flora of the wet flushes and associated tufa deposits bordering the fen and the stream valley. *Primula farinosa*, plentifully flowering, was the showiest member. *Schoenus nigricans* is also conspicuous as a local dominant of the zone just below the moorland edge. Three other species attracting attention were *Plantago maritima*, *Selaginella selaginoides* and a locally plentiful orchid with two colour forms, purplish red and flesh pink, subsequently confirmed as *Orchis latifolia* (*strictifolia*). The zoologists collected in the tarn and becks and on the surrounding land. Though it was not known until later, when specimens had been submitted to Dr H. B. N. Hynes, *Gammarus lacustris* was the most notable zoological discovery. This is a relict known from a small number of lakes in Scotland, North Wales and Yorkshire, but not from the Lake District where extensive search has been made for it. The list of snails taken (*Limnaea pereger*, *Valvata piscinalis*, *V. cristata*, *Planorbis albus*, *P. laevis*, *P. contortus*, *P. crista*) is noteworthy because, although it includes no calciphiles, it is longer than in non-calcareous waters such as those of the Lake District. The outflow stream appeared to be affected by the pollution of the gulls, but the inflow had a number of species of Ephemeroptera that was surprising in view of its small size. Much of it was sandy or gravelly but in places it was just fast enough to have a stony bottom. *Ecdyonurus torrentis* and *Baetis pumilus* were two stony-stream species, *Centroptilum pennulatum*, *C. luteolum*, *Habrophlebia fusca* and *Paraleptophlebia* sp. were all charac-

teristic of slower waters, and burrowers in the genera *Ephemera* and *Caenis* were taken but not identified.

Lunch was followed by an uphill walk to Great Asby Scar, which forms the northern rim of Tarn Moor and is capped by narrow exposures of limestone pavement. Excellent examples of grikes several feet deep were seen closely adjoining turf-covered ground level with the top of the pavement, suggesting at first sight that they are former subsoil fissures whose contents and covering have been removed. Despite the rather small area of ground examined, the grikes yielded a typical 'pavement' list of flora, too long to give in full but characterized by the two following components:

Ferns	'Woodland' angiosperms (herbs)
Asplenium ruta-muraria	*Allium ursinum*
A. trichomanes	*Anemone nemorosa*
A. viride	*Arum maculatum*
Cystopteris fragilis	*Convallaria majalis*
Dryopteris filix-mas	*Endymion nonscriptus*
D. villarsii	*Epilobium montanum*
Phyllitis scolopendrium	*Melica nutans*
Polystichum lobatum	*Mercurialis perennis*
Thelypteris robertiana	*Poa nemoralis*
	Primula vulgaris
	Sanicula europaea

Among the other species, *Mycelis muralis* was conspicuous and *Carex ornithopoda*, in Britain almost restricted to this region, was found. Mist obscured the fine view from this ridge but cleared during the return journey through Shap to Ullswater. Here tea was provided before resumption of the journey back to Windermere over the Kirkstone Pass.

The morning of Monday 16 July was spent at Roudsea Wood National Nature Reserve, which lies at the mouth of the R. Leven 3½ miles north-east of Ulverston. The party was conducted by Dr R. J. Elliott of Merlewood, who is responsible for the management of the wood. Much of it lacks a mature tree canopy owing to felling of standards in both world wars, but re-growth is proceeding and there are obvious natural differences between the parts occupying three types of substratum. The first of these to be encountered was carboniferous limestone, exposed in an old quarry whose unshaded banks and ledges bore an attractive display of calcicolous herbs: *Helianthemum chamaecistus*, *Linum catharticum*, *Inula conyza* and many others, together with *Convallaria majalis* and naturalized *Erinus alpinus*. In the wood itself (where *Convallaria* is also plentiful), the limestone area is marked by a prevalence of ash, together with *Quercus petraea*, and by the occurrence of yew and a rich ground flora including, for instance, *Paris quadrifolia* as an indicator of its general type. The very rare *Carex flava* (*s.s*) was encountered in a wet valley in the limestone area. Before this, however, there had been a detour to a second type of substratum, acid peat, in and adjoining the north-east part of the wood. The latter abuts on to Fish House Moss, the northernmost of the Holker mosses which extend southwards for three miles and represent raised bog somewhat desiccated by drainage, with *Calluna* generally dominant. The ground is still wet enough to carry minor quantities of *Sphagnum* spp., *Narthecium ossifragum* and *Andromeda polifolia*. The peat area incorporated in the wood bears much *Betula pubescens*. A site where a prolonged halt was made has a pure *B. verrucosa* canopy and a continuous field layer of *Vaccinium myrtillus*. Here Dr Ovington of Merlewood demonstrated a layout of small plots where he has recently started experiments with the major nutrients, alone and combined, at low application rates comparable with the accretion from leaf-fall on rich soils. Changes in the surface peat and the flora of the field layer are to be recorded. A lively discussion about the methods and possible limitations had to be curtailed to allow progress towards the south-western side of the wood. Here occurs the third type of substratum, Bannisdale slate, producing an acid soil and *Quercus petraea* woodland with a typical associated flora and fauna. The oaks had been defoliated by *Tortrix viridana* which had often altered the appearance of the under shrubs by spinning up the leaves before pupation. On this side the wood gives way abruptly to brackish and salt marsh beside the estuary.

By the shore in one place, *Centaurium littorale*, *C. minus* and *C. pulchellum* were flowering within a few feet of one another.

The centre for the afternoon was 7 miles to the north-east; to reach it required a drive of more than twice that distance through Cark, Grange and Witherslack. At the destination, Witherslack Woods, Dr Ovington outlined the transect study undertaken to gain some detailed knowledge of these woods as representative of the district and to discover what changes they may undergo. The party then divided into two groups. One group inspected the woodland itself. The trees are taller than in Roudsea Wood: the two main rock substrata are the same. The lower part of the woodland, on Bannisdale slate, is very variable, the vegetation reflecting the variety of soil types, e.g. acid mineral soils, acid peat, and some base-rich peat flushed by water from the limestone escarpment.

The second group walked eastwards through the wood and followed Dr Elizabeth Evans in an intrepid ascent of the limestone scree and loose cliff of Whitbarrow Scar. Yew is plentiful on and especially below the cliff. Above it, in the open, *Epipactis atrorubens* was found in flower. *Helianthemum canum* occurs abundantly along the broken edge. The plateau, about 180 m (600 ft) in altitude, bears expanses of dense grass, largely *Sesleria caerulea* ssp. *calcarea*; but weathered limestone is extensively exposed although not, where seen, in the form of well-developed pavement. Scattered juniper includes old bushes in a moribund condition; some of these seem to be rooted in shallow pockets of soil and emphasize a general appearance on the plateau of vegetational retrogression by active erosion. Plants seen here but not recorded the previous day on Great Asby Scar included *Galium pumilum* and *Thalictrum minus* as well as the orchid and rock-rose already mentioned. The weather, which had been brilliant all day, enhanced the splendid view from this hilltop.

Tea (in view of Scout Scar towards Kendal) did not finish the day's arrangements, for a large number of members gathered at the Grange Hotel for dinner. Formalities were confined to occupation of the Chair by the President (Professor G. C. Varley), who used this appropriate occasion to express the gratitude of the Society to those who had worked so effectively for the success of the meeting. This social function, not a normal feature of summer meetings, seemed to be thoroughly enjoyed.

Tuesday 17 July was devoted to learning on the spot about the work of the Merlewood Research Station. This is so various and vigorous, despite the newness of the establishment (3 years old), that no details can be given here beyond a formal list of the activities explained and demonstrated by the staff, with the aid of excellent exhibits produced amid the difficulties of major plumbing operations in the buildings:

Dr E. M. Evans:	Conservation and land use.
Miss S. Reid:	Library.
Dr O. Gilbert:	Animal nutrition.
Dr J. E. Satchell:	Soil micro-arthropods, etc.
Dr C. K. Capstick:	Soil nematodes.
Dr J. D. Ovington:	Forest soils; long-term production by forest *v.* grassland in hill country; effect of tree-cover on climate.
Mr A. Gordon:	Ecology of regeneration in some Canadian woodlands.
Miss J. C. Brown:	Fungal succession in sand dunes.
Mr J. S. Waid:	Soil microflora.
Dr V. M. Conway and Mr A. Gore:	Moorland research (Moor House).

In the afternoon the members dispersed. The marked success of the meeting was due, as the President had said the previous evening, to the respective Directors (Mr H. C. Gilson and Dr V. M. Conway) and staffs of the F.B.A. Laboratory and the Merlewood Research Station and, in particular, to Mr E. D. Le Cren who had borne the heaviest share in making extremely efficient arrangements.

J. F. HOPE-SIMPSON

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDED 31 DECEMBER 1956

1955	Income	£ s. d.	£ s. d.
	Subscriptions receivable:		
	(Including Arrears and *less* Payments in Advance):		
586	Members taking *Journal of Ecology* only	635 2 9	
323	Members taking *Journal of Animal Ecology* only	331 6 5	
387	Members taking both Journals ...	389 12 7	
5	Associates	5 12 6	
1301		1361 14 3	
	Less Reserve carried forward to 1957 (for second part of *Journal of Animal Ecology*)...	203 10 0	
			1158 4 3
	Interest received:		
162	Investments	162 0 0	
13	Deposit Account...	29 7 10	
73	Post Office Savings Account	72 8 6	
248			263 16 4
	Journal of Ecology:		
	Index to Volumes 1-20		
21	Sales	2 0 0	
8	*Less* Costs	6 0	
13			1 14 0
	Net Deficit for the year transferred to Balance		
62	*Sheet*		823 19 11
1624			£2247 14 6
	Journal of Ecology:		
	Sales:		
1711	Current Volume 44	1846 2 4	
521	Back Volumes and Parts	427 11 1	
216	Reprints of Papers	4 4 0	
—	Return Postage	1 3	
15	Advertising		
40	Contributions to Plates		
2503			2277 18 8
690	*Loss on Journal transferred to Revenue Account*		1597 1 7
3193			£3875 0 3

1955	Expenditure	£ s. d.	£ s. d.
	Working Expenses:		
	Expenses of Meetings	42 8 10	
	Clerical Assistance	14 11 6	
	Audit Fee, etc.	18 7 6	
	Postages, etc.	21 7 2	
	Printing and Stationery	38 15 2	
	Travelling	28 12 10	
	Addressograph, Stencils, etc.	6 1 7	
	Telephone and Telegrams	19 3	
	Bank Charges	1 12 0	
136			172 15 10
	Grants:		
	Freshwater Biological Association ...	10 0 0	
	British Committee for International Nature Conservation	2 2 0	
14			12 2 0
	Journal of Ecology:		
690	Costs *less* Sales		1597 1 7
	Journal of Animal Ecology:		
494	Costs *less* Sales		99 15 6
	Biological Flora of British Isles:		
	Costs	394 19 8	
	Less Sales	29 0 1	
290			365 19 7
1624			£2247 14 6
	Journal of Ecology:		
	Costs:		
2746	Printing, Paper, Blocks and Binding ...		3180 11 1
292	Publishers' Commission		457 11 2
138	Carriage, etc.		220 5 8
3	Editorial Expenses		8 15 5
6	Miscellaneous Expenses		7 16 11
8	Insurance		— — —
3193			£3875 0 3

1163	Current Volume 25, No. 1	666	13	8			
648	Back Volumes and Parts	706	3	0			
103	Reprints of Papers	16	2	9			
1914					1388	19	5
494	*Loss on Journal transferred to Revenue Account*				99	15	6
2408					£1488	14	11

	Printing, Paper, Blocks and Binding:						
2079	Volume 25, No. 1				1072	12	10
225	Publishers' Commission				286	11	4
62	Carriage, etc.				58	17	1
20	Fee for Checking References ...				20	0	0
	Binding Back Issues				35	14	9
14	Insurance						
5	Editorial Expenses				4	17	0
3	Miscellaneous Expenses				10	1	11
2408					£1488	14	11

BALANCE SHEET AS AT 31 DECEMBER 1956

Assets

1955		£	s.	d.	£	s.	d.
	Cash at Bank:						
	At Westminster Bank:						
363	Current Account	702	14	11			
100	Deposit Account	1400	0	0			
					2102	14	11
2897	Post Office Savings Bank Account ...				2969	13	6
	Sundry payment in advance:						
4	(Meeting expenses)				23	4	8
	Publishers Accounts due:						
1099	Index Volume to *Journal of Ecology* ...				1	14	0
25	Sundry Accounts due						
	Commissioners of Inland Revenue:						
26	Income Tax recoverable				38	5	0
	Investments—at cost:						
	£700 of 3% Post Office Savings Bonds 1960/70	700	0	0			
	£300 of 3% Post Office Savings Bonds 1965/75	300	0	0			
	£1000 of 3% Redemption Stock 1986/96	1005	18	6			
	£1200 of 3½% War Stock	1230	4	1			
	£1500 of 4% Federation of Rhodesia & Nyasaland Stock 1972/74	1519	3	0			
4755					4755	5	7
9269					£9890	17	8

Liabilities

1955		£	s.	d.	£	s.	d.
	Members' Subscriptions:						
46	Paid in advance for 1957/62				44	2	11
1	Library Fund				1	5	0
	Publishing Accounts owing to:						
	Blackwell Scientific Publications Ltd.:						
	Journal of Ecology	1592	11	5			
	Journal of Animal Ecology	88	1	6			
	Biological Flora	365	19	7			
799					2046	12	6
	Sundry Accounts owing:						
	Editorial expenses	1	2	6			
	Printing and Stationery	1	1	10			
6					2	4	4
	Reserve of Subscriptions for 1956:						
	(Allocated to second part of *Journal of*						
—	*Animal Ecology*)				203	10	0
	General Revenue Account:						
	Surplus in hand at 31 December 1955	8417	2	10			
	Less Net Deficit for the year ended 31 December 1956	823	19	11			
8417					7593	2	11
9269					£9890	17	8

A further asset, not valued, is the stock of Journals, Index Volumes and Biological Flora Reprints held for the Society by the Publishers.

We have examined the Balance Sheet and Income and Expenditure Accounts of the British Ecological Society as at 31 December 1956, set forth above. We have obtained all the information and explanations we have required, and have verified the investments and Balance at Bank. In our opinion the above Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Society's affairs, according to the best of our information and the explanations given us, and as shown by the books of the Society.

V. S. SUMMERHAYES
C. E. HUBBARD } *Hon. Treasurers*

RYLAND CLIFT & MORRISON, *Incorporated Accountants*
10 ECCLESTON PLACE, WESTMINSTER, S.W.1. 6 *March* 1957

NOTICE TO CONTRIBUTORS

Contributors are asked to study these notes with care in order to save themselves and the editor unnecessary work in the revision of manuscripts.

1. All correspondence should be addressed : **The Editor, Journal of Animal Ecology, The Ferry House, Ambleside, Westmorland.**

2. TEXT. MSS should be typed double-spaced on one side of the paper, leaving top and left-hand margins at least an inch wide. Latin names of genera and species, **but nothing else,** should be underlined. Dates should be in the form '1 Jan. 1956, 25 June' etc., not 'Jan. 1st,' or with the month indicated by a figure. Text-figures are to be referred to as ' Fig. 1 ', etc. In the use of symbols, signs and abbreviations *British Standard 1991: Part I 1954:* should be followed, including the omission of all unnecessary full stops.

The *Journal's* conventions regarding cross-headings should be followed, but they should not be used too freely, **nor should headings be underlined.** Only long papers need include a table of contents. The Royal Society's *General notes on the preparation of scientific papers* should be followed on points not mentioned here.

3. LATIN NAMES. Excepting those of British vertebrates, all Latin specific names should be followed by the authority when the name is first mentioned in the text or tables. Names must be verified either from a standard list such as Kloet and Hincks's *Check-List of British Insects* or by submitting the final MS to the experts who have supplied the identifications.

4. REFERENCES should be listed in alphabetical order at the end of the paper in the form :

Vevers, H. G. & Fisher, J. (1938). The 1938 census of gannets (*Sula bassana*) on Ailsa Craig. *J. Anim. Ecol.* **7,** 303-4.

Titles of journals should be abbreviated according to the *World List of Scientific Periodicals,* except that the English usage of capitals for adjectives should be followed. Any reference not personally seen should be marked with an asterisk. **Nothing** except Latin names of genera and species should be underlined, nor should titles of papers or books be put in inverted commas.

5. TABLES should be set out on separate sheets and numbered in arabic numerals. So far as possible sufficient description should be included in the headings to make tables self-explanatory. The layout of tables should be kept as simple as possible; they are not printed 'boxed'.

6. TEXT-FIGURES. Drawings should be in jet-black indian ink, preferably on Bristol board. Shading must consist of lines or dots, not of half-tone washes. If the addition of mechanical stippling or hatching is required the area should be indicated by hatching lightly in blue pencil. Drawings should be arranged or grouped so that after suitable reduction a figure about 5 in. wide results. Graphs should be drawn on paper ruled in blue or faint grey; axes and graduation marks must be drawn in indian ink. All lettering, numerals and arrows should be shown lightly in pencil for insertion in uniform style by the blockmaker. The author's name and the number of the figure should be written on the back of each. Legends for figures should be collected together at the end of the MS.

7. PLATES. Photographs will only be used to illustrate important points which cannot conveniently be shown in any other way. Unmounted, glossy, half-plate prints showing good detail and moderate, but not excessive, contrast, are required. They should be numbered separately from text-figures, and each print should bear on its back the number and the author's name.

8. PROOFS. Page-proofs only will be sent. They should be returned with the least possible delay, and the minimum of essential correction should be made. Authors are requested to pay particular attention to the checking of numerical matter, mathematical formulae, tables and lists of names.

9. OFFPRINTS. Authors are supplied with 50 offprints gratis. Additional copies may be purchased if ordered when the proofs are returned. Contributors from abroad should order when sending their MSS. Offprints are sent out about a month after publication.